This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.

+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.

+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.

+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

600054827W

C 4 Y 2.

1662 e. 4

A MANUAL

OF

PHYSIOLOGY

A MANUAL

OF

PHYSIOLOGY

FOR THE USE OF

JUNIOR STUDENTS OF MEDICINE

BY

GERALD F. YEO, M.D.DUBL., F.R.C.S.

PROFESSOR OF PHYSIOLOGY IN KING'S COLLEGE, LONDON, ETC.

LONDON
J. & A. CHURCHILL
11, NEW BURLINGTON STREET
1884

C
1662.e.4.
Nat. Sci. 570

BODLEIAN LIBRARY
26 JUN 84
OXFORD.

PREFACE.

THE present volume has been written at the desire on the part of the Publishers that a new elementary treatise on Physiology should be added to the series of admirable students' manuals which they had previously issued.

In carrying this desire into execution I have endeavoured to avoid theories which have not borne the test of time, and such details of methods as are unnecessary for junior students. I do not give any history of how our knowledge has grown to its present standpoint; nor do I mention the names of the authorities upon whose writings my statements depend. I have also omitted the mention of exceptional points, because I find that exceptions are more easily remembered than the main facts from which they differ; and, since we must often be content with the retention of the one or the other, I have tried to ensure that it shall be the more important.

While endeavouring to save the student from doubtful and erroneous doctrines, I have taken great care not to omit any important facts that are necessary to his acquirement of as clear an idea as possible of the principles of Physiology.

I have not hesitated to lay unwonted stress upon those points which many years' practical experience as a teacher and an examiner has shown me are difficult to grasp and are commonly misunderstood; and I have treated such subjects as are useful in the practice of medicine or surgery, more fully than those which are essential only to abstract physiological knowledge.

As medical students are generally obliged to commence the study of Physiology without any anatomical knowledge, I believe it to be absolutely necessary that their first physiological book should contain some account of the structure and relationships of the organs, the functions of which they are about to study. I have therefore added a short account of the construction of the various parts discussed in each chapter; it has, however, been found necessary to curtail this anatomical portion to a mere introductory sketch. Numerous illustrations, with full descriptions attached to each, are introduced to supplement the explanation given in the text.

So far as is consistent with an accurate treatment of the subject, I have avoided technical terms and scientific modes of expression. I know that in attempting to explain physiological truths in every-day language and in a plain common-sense way, I run the risk of appearing to lack the precision that such a subject demands; but after mature consideration I have come to the conclusion that great scientific nicety and a scholastic style of expression have a deterrent effect upon the beginner's industry; and I think it better that he should acquire the first principles of the science in homely language, than pick up technical odds and ends in learned terms, the meaning of which he does not comprehend.

As many words, strange to the first year's student, have to be used and must be learned, it has been thought advisable to add a short glossary, containing an explanation of the most ordinary physiological expressions.

Great difficulty is always found in fixing upon a starting point at which to begin the study of Physiology. To begin *with* the circulation of the blood, which is so essential for the life of every tissue, one should have some knowledge of nerve and muscle. To begin with nerves and muscles the mechanisms and the uses of the blood current should be understood; and so on throughout the various systems, which are so inter-dependent that, for the thorough comprehension of any one, a knowledge of all is required.

I have, therefore, adopted the time-honoured plan of commencing with the vegetative systems and following the course of the aliments to their destination and final application, as I believe that this arrangement is open to as few objections as any other known to me.

I wish here to express my most cordial thanks to many friends who have aided me with kind assistance and advice. I am deeply indebted to Mr. W. Tyrrell Brooks for the great help he afforded me by compiling the chapters on Development; and I feel I cannot sufficiently thank Mr. E. F. Herroun for his untiring and valuable assistance in the revision of the proof sheets.

To Mr. G. Hanlon I am indebted for the careful and skilful manner in which he has executed the new woodcuts, most of which he had to copy from my rough drawings.

King's College, London,
January, 1884.

CONTENTS.

CHAPTER I.

The Objects of Physiology.

PAGE
Introductory Definitions 1
Structural and Physical Properties of Organisms 4
Chemical Composition 5
Vital Phenomena 6

CHAPTER II.

General View of the Structure of Animal Organisms.

Cells 8
Protoplasm, Nucleus, Cell-wall 10
Cell-contents 11
Varieties of Cells 12
Modifications of Original Cell-tissues 13
- I. Epithelial Tissues 17
- II. Nerve Tissues 20
- III. Muscle or Contractile Tissues 23
- IV. Connective Tissues 25

CHAPTER III.

Chemical Basis of the Body.

Elements in the Body 33
Classification of Ingredients found in the Tissues 35
Plasmata 35
Albuminous Bodies 37
Classification of Albumins 38
Albuminoids 41

PAGE
Products of Tissue Change 42
Carbohydrates 46
Fats 47
Inorganic Bodies 48

CHAPTER IV.

THE VITAL CHARACTERS OF ORGANISMS.

Protoplasmic Movements 51
Reproduction 54
Bacteria 57
Amœba 59
Paramæcium 61

CHAPTER V.

NUTRITION AND FOOD STUFFS.

Classification of Foods 66
Composition of Special Forms of Food 68
Milk 69
Cheese, Meat, Eggs, &c. 71
Vegetables 73

CHAPTER VI.

THE MECHANISM OF DIGESTION.

Mastication 77
Deglutition 78
Nervous Mechanism of Deglutition 83
Vomiting 85
Movements of the Intestines 87
Defæcation 89
Nervous Mechanism of the Intestinal Motion 91

CHAPTER VII.

MOUTH DIGESTION.

Salivary and Mucous Glands 94
Characters of Mixed Saliva 97
Nervous Mechanism of Secretion of Saliva 99
Changes in the Gland-cells 104
Functions of the Saliva 107

CHAPTER VIII.

THE STOMACH DIGESTION.

PAGE
The Gastric Glands 110
The Characters of Gastric Juice 112
Mode of Secretion of Gastric Juice 113
Action of the Gastric Juice 115

CHAPTER IX.

PANCREATIC JUICE.

Structure of the Pancreas 120
Characters and Mode of Secretion of Pancreatic Juice . . . 121
Changes in the Gland-cells 123
Action of Pancreatic Juice on Proteids 124
Action on Fats 125
Action on Starch 126

CHAPTER X.

BILE.

Functions of the Liver 127
Structure of the Liver 128
Composition and Method of obtaining Bile 133
Method of Secretion of Bile 136
Functions of the Bile 138

CHAPTER XI.

FUNCTIONS OF THE INTESTINAL MUCOUS MEMBRANE.

Structure of the Small Intestines 140
Method of obtaining Intestinal Secretion 142
Characters and Functions of the Intestinal Juice 143
Functions of the Large Intestine 145
Putrefactive Fermentations in the Intestine 146

CHAPTER XII.

ABSORPTION.

Interstitial Absorption 149
The Lymphatic System 150

PAGE
Structure of Lymphatic Glands 151
Intestinal Absorption 155
Mechanism of Absorption 159
Materials Absorbed 160
Lymph and Chyle 163
Movement of the Lymph 165

CHAPTER XIII.

THE CONSTITUTION OF THE BLOOD AND THE BLOOD-PLASMA.

General Characters of the Blood 168
Amount of Blood in the Body 169
Physical Construction of the Blood, Blood-plasma 171
Chemical Composition of Plasma 173
Preparation and Properties of Fibrin 175
Serum 176

CHAPTER XIV.

BLOOD CORPUSCLES.

Proportion of Red to White 177
White Blood-cells 178
Origin of the Colourless Blood-cells 180
The Red Corpuscles, Sizes and Shapes 181
Action of Reagents on Red Corpuscles 183
Method of counting Corpuscles 185
Chemistry of the Colouring Matter of the Blood 187
Spectra of Hæmoglobin 189
Hæmatin, Hæmin, &c. 191
Development of the Red Disks 192
The Gases of the Blood 193

CHAPTER XV.

COAGULATION OF THE BLOOD.

Formation of the Blood-clot 195
Circumstances influencing Coagulation 197
The Cause of Coagulation 199
Coagulation in the Vessels 200
Formation of Fibrin 201

CHAPTER XVI.

THE HEART.

PAGE
Pulmonary and Systemic Circulations 203
Method of the Circulation of the Blood 204
The Heart 206
Arrangement of Muscle Fibres 208
Minute Structure of the Heart 209
Action of the Valves 211
Movements of the Heart 213
Cycle of the Heart-beat 214
The Heart's Impulse 216
Heart-sounds 218
Innervation of the Heart 220
Local Centres 221
Inhibitory Nerves 224
Acceleration Nerves 225
Afferent Cardiac Nerves. 226

CHAPTER XVII.

THE BLOOD-VESSELS.

Structure of the Vessels 227
The Capillaries 229
Relative Capacity of the Vessels 231
Physical Forces of the Circulation 232
The Blood-pressure 234
Measurement of Blood-pressure 237
Variations in the Blood-pressure 241
Influence of Respiration on the Blood-pressure 242
The Arterial Pulse 247
Methods of obtaining Pulse-tracings 248
Variations in the Pulse 251
Velocity of the Blood-current 252
Controlling Mechanisms of the Blood-vessels 255

CHAPTER XVIII.

THE MECHANISM OF RESPIRATION.

Gas Interchange 260
Structure of the Lungs and Air-passages 263
The Thorax 265
Thoracic Movements 267

PAGE
Inspiratory Muscles . . . 269
Expiration . . . 273
Function of the Pleura . . . 274
Pressure Differences in the Air . . . 275
The Volume of Air . . . 276
Nervous Mechanism of Respiration . . . 278
Modified Respiratory Movements . . . 283

CHAPTER XIX.

The Chemistry of Respiration.

Composition of the Atmosphere . . . 285
Expired Air . . . 286
Changes the Blood undergoes in the Lungs . . . 288
Gases in the Blood . . . 289
Internal Respiration . . . 292
Respiration of Poisonous Gases . . . 293
Ventilation . . . 294
Asphyxia . . . 295

CHAPTER XX.

Blood-elaborating Glands.

Ductless Glands . . . 298
Supra-renal Capsule and Thyroid Body . . . 299
Thymus . . . 300
Spleen . . . 301
Functions of the Spleen . . . 302
Glycogenic Function of the Liver . . . 305
Glycogen . . . 307

CHAPTER XXI.

Secretions.

Lachrymal Glands . . . 309
Mucous Glands . . . 310
Sebaceous Glands . . . 311
Mammary Glands . . . 312
Composition of Milk . . . 314
Sudoriferous Glands . . . 317
Cutaneous desquamation . . . 319

CHAPTER XXII.

URINARY EXCRETION.

PAGE
Structure of the Kidneys 321
Blood-vessels of the Kidneys 323
Urine 325
Method of Secretion of the Urine 326
Chemical Composition of Urine 329
Urea 330
Uric Acid 331
Kreatinin, Xanthin, Hippuric Acid, Oxalic Acid, &c. . . . 332
Colouring Matters and Inorganic Salts 333
Abnormal Constituents 334
Urinary Calculi 335
Source of Urea, &c. 336
Nervous Mechanism of the Urinary Secretion 338
Outflow of Urine 339
Nervous Mechanism of Micturition 341

CHAPTER XXIII.

NUTRITION.

Tissue Changes during Starvation 344
Food Requirements 347
Ultimate Uses of Food Stuffs 351

CHAPTER XXIV.

ANIMAL HEAT.

Warm- and Cold-blooded Animals 353
Variations in the Body Temperature 354
Mode of Production of Animal Heat 356
Income and Expenditure of Heat 357
Maintenance of Uniform Temperature 359

CHAPTER XXV.

CONTRACTILE TISSUES.

Histology of Muscle 366
Properties of Muscle in the Passive State 368
Electric Phenomena of Muscle 371

PAGE
Active State of Muscle 374
Muscle Stimuli 375
Changes occurring in Muscle on its entering the Active State . . 377
Muscle Contraction 381
Graphic Method of recording Contraction 382
Tetanus, Fatigue, &c. 388
Rigor Mortis 393
Unstriated Muscle 395

CHAPTER XXVI.

THE APPLICATION OF SKELETAL MUSCLES.

General Arrangements 396
Joints 397
Standing 399
Walking and Running 402

CHAPTER XXVII.

VOICE AND SPEECH.

Anatomical Sketch 404
Mechanism of Vocalisation 406
Properties of the Human Voice 409
Nervous Mechanism of Voice 410
Speech 411

CHAPTER XXVIII.

GENERAL PHYSIOLOGY OF THE NERVOUS SYSTEM.

Anatomical Sketch 413
Functional Classification 415
Chemistry and Electric Properties of Nerves 416
The Active State of Nerve-fibres 417
Nerve Stimuli 418
Velocity of Nerve-impulse 420
The Electric Changes in Nerves 421
Electrotonus 422
Irritability of Nerve Fibres 423
Law of Contraction 426
Nerve Corpuscles and Terminals 428
Functions of the Nerve Cells 430

CHAPTER XXIX.

SPECIAL PHYSIOLOGY OF NERVES.

PAGE
Spinal Nerves 433
The Cranial Nerves 434
The Trochlear Nerve, Portio Dura, &c. 435
Efferent and Afferent Fibres 439
Ganglia of the Fifth Nerve 441
The Glosso-pharyngeal Nerve 442
The Vagus Nerve 443
The Hypoglossal Nerve 445

CHAPTER XXX.

SPECIAL SENSES.

Skin Sensations 448
Nerve Endings 449
Sense of Locality 452
Sense of Pressure 454
Temperature Sense 455
General Sensations 457

CHAPTER XXXI.

TASTE AND SMELL.

Sense of Taste 460
Sense of Smell 463

CHAPTER XXXII.

VISION.

The Construction of the Eye-ball 466
Dioptric Media of the Eye-ball 469
Structure of the Lens 471
The Dioptrics of the Eye 473
Accommodation 478
Defects of Accommodation 480
Defects of Dioptric Apparatus 481
The Iris 482
The Ophthalmoscope 485
Visual Impressions 486

PAGE
The Function of the Retina . . . 487
Colour Perceptions . . . 493
Mental Operations in Vision . . . 495
Movements of the Eye-balls . . . 496
Binocular Vision . . . 498

CHAPTER XXXIII.

HEARING.

Sound . . . 499
Conduction of Sound-vibrations through the Outer Ear . . . 502
Conduction through the Tympanum . . . 505
Conduction through the Labyrinth . . . 507
Stimulation of the Auditory Nerve . . . 510

CHAPTER XXXIV.

CENTRAL NERVOUS ORGANS.

Nerve Cells . . . 513
The Spinal Cord as a Conductor . . . 515
The Spinal Cord as a Collection of Nerve Centres . . . 518
Special Reflex Centres . . . 525
Automatism . . . 526

CHAPTER XXXV.

THE MEDULLA OBLONGATA.

The Medulla Oblongata as a conductor . . . 528
The Respiratory Centre . . . 530
The Vaso-motor Centre . . . 531
The Cardiac Centre . . . 533

CHAPTER XXXVI.

THE BRAIN.

The Mesencephalon and Cerebellum . . . 535
Crura Cerebri . . . 537
Basal Ganglia . . . 538
Cerebral Hemispheres . . . 541
Localisation of the Cerebral Functions . . . 542

CHAPTER XXXVII.

REPRODUCTION.

PAGE
Origin of Male and Female Generative Elements 546
Menstruation and Ovulation 549
Changes in the Ovum subsequent to Impregnation 551
Formation of the Membranes 555
The Placenta 561

CHAPTER XXXVIII.

DEVELOPMENT.

Development of the Vertebral Axis 566
Development of the Central Nervous System 571
The Alimentary Canal and its Appendages 576
The Genito-urinary Apparatus 581
The Blood-vascular System 587
Development of the Eye 600
Development of the Ear 604
Development of the Skull and Face 606

GLOSSARY 611

INDEX 620

COMPARISON OF THE METRICAL WITH THE COMMON MEASURES.

By Dr. Warren De la Rue.

MEASURES OF LENGTH.

	In English Inches.	In English Feet = 12 Inches.	In English Yards = 3 Feet.	In English Fathoms = 6 Feet.	In English Miles = 1,760 Yards.
Millimeter	0·03937	0·0032809	0·0010936	0·0005468	0·0000006
Centimeter	0·39371	0·0328090	0·0109363	0·0054682	0·0000062
Decimeter	3·93708	0·3280899	0·1093633	0·0546816	0·0000621
Meter	39·37079	3·2808992	1·0936331	0·5468165	0·0006214
Decameter	393·70790	32·8089920	10·9363310	5·4681655	0·0062138
Hectometer	3937·07900	328·0899200	109·3633100	54·6816550	0·0621382
Kilometer	39370·79000	3280·8992000	1093·6331000	546·8165500	0·6213824
Myriometer	393707·90000	32808·9920000	10936·3310000	5468·1655000	6·2138244

1 Inch = 2·539954 Centimeters. | 1 Foot = 3·0479449 Decimeters. | 1 Yard = 0·91438348 Meter. | 1 Mile = 1·6093149 Kilometers.

MEASURES OF CAPACITY.

	In Cubic Inches.	In Cubic Feet = 1,728 Cubic Inches.	In Pints = 34·65923 Cubic Inches.	In Gallons = 8 Pints = 277·27384 Cubic Inches.	In Bushels = 8 Gallons = 2218·19075 Cubic Inches.
Milliliter or cubic centimeter	0·061027	0·0000353	0·001761	0·00022010	0·000027512
Centiliter or 10 cubic centimeters	0·610271	0·0003532	0·017608	0·00220097	0·000275121
Deciliter or 100 cubic centimeters	6·102705	0·0035317	0·176077	0·02200967	0·002751208
Liter or cubic decimeter	61·027052	0·0353166	1·760773	0·22009668	0·027512085
Decaliter or centistere	610·270515	0·3531658	17·607734	2·20096677	0·275120846
Hectoliter or decistere	6102·705152	3·5316581	176·077341	22·00966767	2·751208459
Kiloliter or stere, or cubic meter	61027·051519	35·3165807	1760·773414	220·09667675	27·512084594
Myrioliter or decastere	610270·515194	353·1658074	17607·734140	2200·96676750	275·120845937

1 Cubic Inch = 16·3861759 Cubic Centimeters. | 1 Cubic Foot = 28·3153119 Cubic Decimeters. | 1 Gallon = 4·543457969 Liters.

MEASURES OF WEIGHT.

	In English Grains.	In Troy Ounces = 480 Grains.	In Avoirdupois Lbs. = 7,000 Grains.	In Cwts. =112 Lbs. =784,000 Grains.	Tons = 20 Cwt. =15,620,000 Grains.
Milligram	0·015432	0·000032	0·0000022	0·00000002	0·000000001
Centigram	0·154323	0·000322	0·0000220	0·00000020	0·000000010
Decigram	1·543235	0·003215	0·0002205	0·00000197	0·000000098
Gram	15·432349	0·032151	0.0022046	0·00001968	0·000000984
Decagram	154·323488	0·321507	0·0220462	0·00019684	0·000009842
Hectogram	1543·234880	3·215073	0·2204621	0·00196841	0·000098421
Kilogram	15432·348800	32·150727	2·2046213	0·01968412	0·000984206
Myriogram	154323·488000	321·507267	22·0462126	0·19684118	0·009842059

CORRESPONDING DEGREES IN THE FAHRENHEIT AND CENTIGRADE SCALES.

Fahr.	Cent.	Cent.	Fahr.
500°	260°·0	100°	212°·0
450°	232°·2	98°	208°·4
400°	204°·4	96°	204°·8
350°	176°·7	94°	201°·2
300°	148°·9	92°	197°·6
212°	100°·0	90°	194°·0
210°	98°·9	88°	190°·4
205°	96°·1	86°	186°·8
200°	93°·3	84°	183°·2
195°	90°·5	82°	179°·6
190°	87°·8	80°	176°·0
185°	85°·0	78°	172°·4
180°	82°·2	76°	168°·8
175°	79°·4	74°	165°·2
170°	76°·7	72°	161°·6
165°	73°·9	70°	158°·0
160°	71°·1	68°	154°·4
155°	68°·3	66°	150°·8
150°	65°·5	64°	147°·2
145°	62°·8	62°	143°·6
140°	60°·0	60°	140°·0
135°	57°·2	58°	136°·4
130°	54°·4	56°	132°·8
125°	51°·7	54°	129°·2
120°	48°·9	52°	125°·6
115°	46°·1	50°	122°·0
110°	43°·3	48°	118°·4
105°	40°·5	46°	114°·8
100°	37°·8	44°	111°·2
95°	35°·0	42°	107°·6
90°	32°·2	40°	104°·0
85°	29°·4	38°	100°·4
80°	26°·7	36°	96°·8
75°	23°·9	34°	93°·2
70°	21°·1	32°	89°·6
65°	18°·3	30°	86°·0
60°	15°·5	28°	82°·4
55°	12°·8	26°	78°·8
50°	10°·0	24°	75°·2
45°	7°·2	22°	71°·6
40°	4°·4	20°	68°·0
35°	1°·7	18°	64°·4
32°	0°·0	16°	60°·8
30°	— 1°·1	14°	57°·2
25°	— 3°·9	12°	53°·6
20°	— 6°·7	10°	50°·0
15°	— 9°·4	8°	46°·4
10°	—12°·2	6°	42°·8
5°	—15°·0	4°	39°·2
0°	—17°·8	2°	35°·6
— 5°	—20°·5	0°	32°·0
—10°	—23°·3	— 2°	28°·4
—15°	—26°·1	— 4°	24°·8
—20°	—28°·9	— 6°	21°·2
—25°	—31°·7	— 8°	17°·6
—30°	—34°·4	—10°	14°·0
—35°	—37°·2	—12°	10°·4
—40°	—40°·0	—14°	6°·8
—45°	—42°·8	—16°	3°·2
—50°	—45°·6	—18°	—0°·4
		—20°	—4°·0

ERRATUM.

Page 123, line 4 from bottom, for "*steopsin*" read "*steapsin*."

MANUAL OF PHYSIOLOGY.

CHAPTER I.

THE OBJECTS OF PHYSIOLOGY.

BIOLOGY, the science which deals with living beings and the phenomena exhibited by them, may be divided into two great branches, viz. :—

1. Morphology, which treats of the forms and structure of the bodies of living creatures :

2. Physiology, which attempts to explain the modes of activity exhibited by them during their life-time, and may therefore be defined as the science which investigates the phenomena presented by the textures and organs of healthy living beings ; or, in short, the study of the actions of organisms in contradistinction to that of their shape and structure.

The organic or living world is naturally divided into the Animal and Vegetable kingdoms. We have, therefore, both animal and vegetable morphology and physiology. In studying the vegetable kingdom, the form, and the structure, as well as the activity of plants are associated together in the science known as Botany. The physiology of plants may therefore here be omitted ; though, indeed, it cannot be neglected in considering the processes belonging to animal life. On the other hand, the morphology and the physiology of animals are commonly taught separately, and in the medical curriculum are made distinct subjects.

Morphology properly includes the external form, the general construction or anatomy of organisms, and the minute structure of their textures as revealed by the microscope. This latter branch of study, under the name Histology, has now developed into a very wide subject, which is inseparable from either physiology or anatomy. In this country histology is commonly taught in the medical schools with physiology, for while the time of the teachers of morphology is occupied in expounding the details of descriptive anatomy, the microscope is in everyday use in the physiological laboratory. Moreover, an adequate knowledge of microscopic methods, and of the various form-elements of the different textures of the body is one of the first essentials for physiological study.

As the different actions of the body are performed by different tissues, which in the higher animals are grouped together as distinct organs, a general idea of the position and construction of these different parts of the body must be acquired before the study of physiology can be commenced. Anatomy and general morphology are the frameworks upon which physiological knowledge is built up. Some knowledge of these subjects must therefore precede the study of physiology, in order that the student may be in a position to grasp even the simplest facts connected with any physiological question.

We shall soon find that the assistance of other sciences is also indispensable to physiology. Thus every action of a living texture or tissue is accompanied by some chemical change, the chemical process in fact being commonly the essential part of the phenomenon. The student of physiology must, then, know something of the science of chemistry; indeed the mode of action of chemical elements forms quite as important a groundwork for the study of the activity of the living tissues as their general form or minute structure.

Further, the laws which govern the motions of inanimate bodies also control the actions of living tissues, for we cannot claim to understand or recognise the existence of any laws affecting living organisms other than those known to be applicable to dead matter. There are a great number of activities shown by living textures which we cannot explain by the recognised laws of nature. We therefore use, for convenience sake, the term "vital phenomena," to indicate processes which are beyond our present chemical and physical knowledge. In using this term we must not think it implies a separate set of laws of life. We cannot discover or formulate any special laws affecting living beings only, and therefore we must not assume that any such exist. We must rather endeavour to explain all the so-called "vital phenomena" by means of the laws known to chemists and physicists. By this means we shall certainly get a closer insight into the processes of life, and if there be laws governing the living beings we may learn to know them. This method of working has already given good results, for within comparatively recent times many of the processes which were regarded as specially vital in character have been shown to be within the power of the experimenter and to depend on purely physico-chemical processes.

It is therefore necessary for the physiologist, before he attempts to explain the activities of any organism, to be familiar with not only the structure of its body but also the various laws which, as chemists and physicists teach us, control the operations of inanimate matter.

The sciences of chemistry and physics may, in fact, be regarded as the physiology of inorganic matter, just as when chemistry and physics are applied to the elucidations of the functions of living creatures by the biologist, the study is called physiology. When we consider how far the chemist and the physicist still are from thoroughly grasping and interpreting all the phenomena presented by the various kinds and conditions of matter, we cannot be surprised that those who attempt to explain the actions of living beings find many processes that they are unable to comprehend. But while physiologists frequently make use of the convenient term "vital phenomena," they do not thereby imply the existence of a special living force or any kind of energy peculiar to living creatures.

The final end of physiology is, then, not yet within the reach of our modern methods of research. To explain the mode of activity of living beings, and grasp the exact relation borne by their living phenomena to the laws which govern them, is a task of enormous difficulty. Indeed the manifestations of certain energies in living organisms are so complicated that it is often, if not generally, impossible to say exactly how they are brought about, and we are therefore obliged, for the present at least, to be satisfied with the mere recognition and description of the phenomena.

Since the human organism is the special study of students of medicine, the contents of this volume should properly be restricted to the physiology of man. But human physiology cannot be studied alone; because in man we cannot watch sufficiently closely, or question fully, by experiment, the phenomena of life. Further, no sharp line of separation can be drawn between the actions of the various organs of man and those of the lower animals. The consideration of the physiology of those animals which are akin to man must therefore go hand in hand with the study of the physiology of man himself. Much light has been thrown on the actions of the most complex textures of the highest animals, by the observation of the activities of the lowest organisms, where the manifestations of life may be carefully watched with the microscope in the living animal under perfectly normal conditions.

GENERAL CHARACTERS OF ORGANISMS.

The term organism, which is commonly used as having the same meaning as *living being*, owes its derivation to the complexity of structure common among the higher forms of life, which are made up of several distinct organs. This organic construction no longer holds good as a distinguishing mark between living beings and inanimate matter, because we are acquainted with a vast number of living organisms, both plants and animals, which are not made up of organs, but are composed of a minute piece of a soft jelly-like material, which is simply granular throughout, and devoid of structural differentiation during the life of the creature.

We may classify the general characters of living beings as follows :

1. Structural and physical properties.
2. Chemical composition.
3. Activities during life (vital phenomena).

1. STRUCTURAL CHARACTERS OF ORGANISMS.—The minute structure of living beings as shown by the microscope no doubt helps to distinguish the textures of organisms from inorganic structures. Although organic textures are found to differ very widely in their characters they are all related in one respect, namely, that at some period of their existence they consisted of cells, *i.e.*, minute masses of a substance called *Protoplasm*. In plants this cellular structure remains obvious in nearly all parts of the adult organism, no matter how much the texture may be modified by adaptation to the requirements of any given duty or function. If we examine with the microscope the leaves, bark, wood, or pith of a plant, in all of them a cellular structure can be recognised. In the less developed members of the animal kingdom, and during the initial stages in the existence of the highest animals, the textures are composed exclusively of aggregations of living cell-elements. We shall shortly see that in the more fully developed condition of the higher animals, the cells become variously modified in form and function, and the protoplasm manufactures various structures adapted to the performance of the diverse functions of the different parts. In all organic textures which can be said to be living, cells are dispersed in greater or less number throughout them, and regulate their nutrition and repair.

2. CHEMICAL COMPOSITION.—There are no characters in the chemical composition of the textures of organic beings which can be said to be absolutely distinctive or to separate them from inorganic matter. No doubt their chemical construction commonly exhibits

certain peculiarities, not seen in dead matter, which may be taken as characteristic, but living textures only differ in the general plan of arrangement and composition from that most commonly met with in the construction of inorganic materials.

In the first place, the great majority of the *chemical elements* which we know of, take no share in the formation of living creatures, and are never found to enter into their composition. Practically only fifteen of the sixty-three elements known to chemists take part in making up the tissues of animals. The majority of these are only present in very small quantity and with no great constancy. On the other hand, there are four elements, namely, carbon, oxygen, hydrogen, and nitrogen, which are found with such great regularity, and in so great quantity, that they may be said to make up the great bulk (97 per cent.) of the animal frame. The great constancy with which the first three of these elements occurs must be regarded as the most important character of organic tissues.

Secondly, in organic textures the chemical elements are associated in a much more complex and irregular proportion. Generally a large number of *atoms*, of each element, are grouped together to form the *molecule*, and often the compound is so complex that its chemical formula remains a matter of doubt. As an example, a remarkable body, called lecithin, which appears in the analysis of protoplasm and many tissues, may be mentioned; it is a peculiar compound containing nitrogen and phosphorus, and in construction said to be like a fat. It may be expressed thus :—

$$C_{44}\,H_{90}\,N\,PO_{9}.$$

In inorganic substances, on the other hand, the elements are found to be combined, as a general rule, in simple and regular proportions. The molecules are made up of but few elements arranged in a definite manner and firmly bound together, so that they are not prone to undergo spontaneous decomposition. As an example, we may take water, which has the well-known formula,

$$H_2O.$$

Though these bodies may be taken as types of organic and inorganic substances respectively, it must not be imagined that all organic bodies are as complex, irregular, and unstable as lecithin, or that inorganic compounds, as a rule, are invariably simple and stable like water.

It is further remarkable that *Carbon*—an element which is exceptional in forming but few associations in the mineral world, where it chiefly combines with oxygen to form CO_2—is almost invariably present in living textures, in which it is combined with hydrogen and nitrogen as well as oxygen in various proportions. The constancy of carbon as an ingredient of organic bodies is so great that what formerly was called organic chemistry is now often called the chemistry of the carbon compounds.

These complex associations of many atoms of carbon with many atoms of other elements, are readily dissociated when exposed to the air under even slightly disturbing influences. When heated to a certain degree they burn, *i.e.*, unite rapidly with the oxygen of the air, and in the presence of minute organisms they putrefy. Thus *instability* is a general feature commonly met with in most substances of organic origin.

Chemical instability reaches the highest pitch in tissues which are actually alive and engaged in vital processes. So long as any texture lives it must constantly undergo certain chemical changes, one of which is regarded as a kind of decomposition, tending to produce disintegration, and the other, a re-integration by means of new chemical associations with fresh materials. A tissue may then be said to deserve the term living, only as long as it undergoes these antagonistic chemical changes. The tendency to destructive oxidation or disintegration is intimately connected with the functional activity of the living texture and increases with this activity. The re-integration or constructive process requires the presence of suitable materials with which the texture may combine, in order to make up for the loss. Thus living tissues are ever on the point of destruction, which can only be warded off by the timely reconstruction of their chemical ingredients by suitable fresh materials. This reconstruction by means of fresh matter from without is called *assimilation*, and forms the most, if not the only, satisfactory criterion by which adequately to distinguish living beings from inorganic matters.

The whole object of all these chemical processes is to supply suitable fresh materials to the various textures for their assimilation. This will be found to form a great part of physiological study. Further, the energy manifested in the living activity of the textures depends upon the various oxidising processes, and the exact laws which govern these combustions, and the results they give rise to in the various tissues, practically make up the other part of physiology.

3. VITAL PHENOMENA.—The so-called vital phenomena which take place in the textures of organisms are, for the most part, performed by the agency of the living cell-elements, in which we can re-

cognise independent manifestations of life, such as the response to stimuli, motion, nutrition, growth, &c. The living activity of organisms requires for its perfect development certain external conditions, namely, a certain degree of warmth and *moisture*. Without heat and moisture the chemical interchanges just mentioned cannot go on, and the organism is either destroyed or remains in a state of inactivity.

The nutrition of the animal body which is accomplished by means of the processes of assimilation already mentioned enables it to grow, and, up to a certain point, increase in size, and further to undergo many changes in form and texture. There is, however, a limit to this assimilative power: nutrition loses in activity, growth gradually stops, and after a time decay appears and is followed by death.

Thus organisms exist only for a limited period of time, during which their size, form, and functional activity are constantly undergoing some alteration dependent on the incessant changes in their molecular construction.

This cycle of changes through which organisms pass we speak of as their life-time. During this life-time, at the period when their functional activity is at its height, they possess the remarkable faculty of producing individuals like themselves.

This is accomplished by setting apart a cell which, under favourable circumstances, assumes special powers of growth, increases in size by the rapid formation of new cells, and developes into an independent living unit. In time it arrives at maturity, and becomes like its parent, and then passes through the same cycle—by its power of assimilation it grows to maturity, reproduces its like, decays, and dies.

CHAPTER II.

GENERAL VIEW OF THE STRUCTURAL CHARACTERS OF ANIMAL ORGANISMS.

The parts played in Physiology by cells are so many and so important that it is necessary at the very outset to consider their properties somewhat in detail.

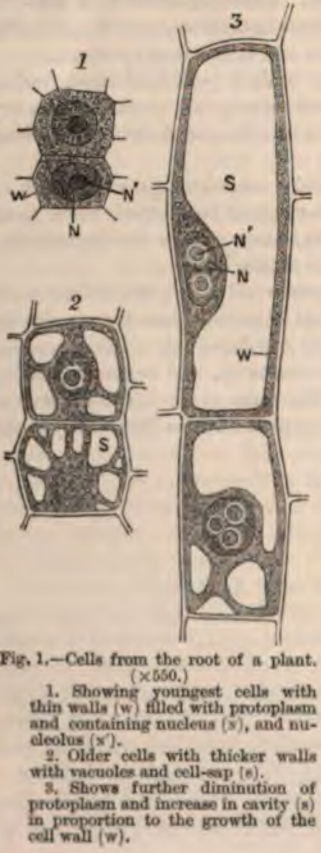


Fig. 1.—Cells from the root of a plant. (×550.)

1. Showing youngest cells with thin walls (W) filled with protoplasm and containing nucleus (N), and nucleolus (N').

2. Older cells with thicker walls with vacuoles and cell-sap (S).

3. Shows further diminution of protoplasm and increase in cavity (S) in proportion to the growth of the cell wall (W).

The demonstration of the cellular structure of plants was first made in 1832 by a distinguished German botanist named Schleiden, who considered the cells to be characteristic of plant tissue. A few years later Schwann showed that the animal tissues were also made up of cells, though not so completely, and that they owed their origin and development to cell elements. Thus originated the cellular theory, which, with some modification, is now the basis of all physiological enquiry.

The first idea which was conveyed by the term *cell* varied much from that which we now accept as a proper definition of such an organic unit.

Vegetable cells being the first discovered were taken as the type of all. The main characteristics of these may be briefly summed up. Firstly, a membranous sac called the *cell wall*, generally very well defined, and secondly, within the cell wall various *cell contents*. Among the more conspicuous portion of the latter may be mentioned the (1) nucleus, which lies in a soft, clear, jelly-like substance called protoplasm, and (2) certain cavities called vacuoles, which are filled with a clear fluid or "cell sap."

Further investigation of the life history of cells, particularly in the early stages of their development, showed that the cell wall, which played so important a part in the original conception of a cell was not always present, but was formed by the protoplasm in the later stage of growth. The cell sap and other matters were found less commonly present, and appeared still later in the life-time of the vegetable cell; hence it was concluded that they were the outcome of changes due to the activity of the protoplasm, and that this latter was the only real essential and vital part of the cell.

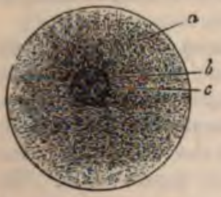


Fig. 2.—Diagram of animal cell (ovum). (Gegenbauer.)

a. Granular protoplasm.
b. Nucleus.
c. Nucleolus.

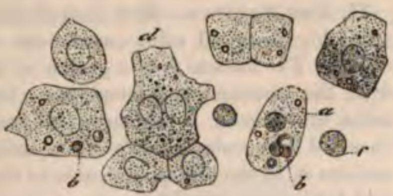


Fig. 3.—Liver cell of man, containing fat globules (*b*) and biliary matters. (Cadiat.)

Subsequently, from the fact that some vegetable cells in the youngest and most active stage of their growth have no limiting wall, and that most animal cells have none during any part of their life, it was proposed to define a cell as a mass of protoplasm containing a nucleus. But further research showed that the nucleus was not always present. In many cryptogamic plants no nucleus can be found, and in some animal cells, which must be regarded as independent individuals (Protamœba), there is no nucleus at any part of its life-time. This would lead us to suppose that *a mass of protoplasm capable of manifesting all the phenomena of life* would be a sufficient definition. Though this is probably correct in a few cases, the vast majority of cells do contain nuclei. As it is difficult to divest our minds of the connexion between the two, it has been proposed to give the name *cytode* to the non-nucleated forms, which certainly are very exceptional, reserving the term *cell* for the common nucleated unit. Each part of the cell may now be considered in the order of its importance, viz., protoplasm, nucleus, cell wall, and cell contents.

I. Protoplasm is a colourless, pale, milky, semi-translucent substance, more or less altered in appearance by various foreign matters which lie in it. These latter also give it a granular appearance, and when dead it commonly exhibits a linear marking or fine network. During life its consistence is nearly fluid, varying with the circumstances in which it is placed, from that of a gum solution to a soft jelly. When living unmolested in its normal medium it seems to flow into various shapes, but this is a living action which does not prove it to be diffluent, for any attempt to investigate it by experiment causes a change in its consistence approaching to rigidity.

As the full comprehension of the function of this substance lies at the root of the greater part of Physiology, the reader is referred for a detailed account of its properties to Chapter III. on Vital Phenomena, where it will be discussed at greater length.

II. The Nucleus.—Most independent masses of protoplasm, and all highly organized cells, contain one or more nuclei in their substance. The nucleus is in a greater or less degree sharply divided off from the surrounding protoplasm. Its presence can generally be made much more conspicuous by treating the cell with various chemical re-agents, notably dilute acids and certain dyes. The nucleus is, in the former case, able to resist the action of dilute acetic acid for a much greater length of time than the remainder of the cell, so that it stands out clearly, while the rest becomes quite transparent. In the latter case, magenta (one of the aniline dyes) stains the nucleus sooner and deeper than the protoplasm. Although it has been accredited with special independent movements, it may safely be said that in comparison with the protoplasm it is not very contractile. Yet it appears to be intimately associated with the vital phenomena of the cell, and may be said to control or initiate the most important activities of the cell, namely, its division. The small size of the nucleus adds greatly to the difficulty of investigating its functions, and much remains to be made out concerning both its structure and properties, although recently considerable progress has been made in this direction.

III. The Cell Wall.—It has already been stated that the most active form-elements, such as the cells in the earliest stages in the life of an organism (embryonic cells), have no enclosing membrane or cell wall. But in the more advanced stages of cell life we find this second form of protoplasmic differentiation to be common enough. In animal cells the limiting membrane has never the same importance as the cell wall in vegetable tissues, where some of the principal textures may be traced to a direct modification of the cell wall, still recognisable as such. Whenever such a limiting membrane does exist, it is always formed by the outer layers of protoplasm undergoing changes so as to become of greater consistence. In the animal tissues the protoplasmic units form various structures, which, however, do not hold the relation to them of limiting membranes, but rather give the idea of lying between the cells. Hence, in one large group of tissues, they have been called *intercellular substance*, while in others they appear as materials specially modified for the furtherance of the functions of the special tissues.

IV. Cell Contents.—Regarding protoplasm as the essential living part of the cell, under this heading will come only those extraneous matters which are the outcome of protoplasmic activity.

The cell contents which are present with such constancy and in such variety in vegetable cells, form in them an all-important part; but in most animal cells the contents do not occupy such a striking position.

No doubt animal protoplasm is quite as capable as that of vegetables of making out of its own substance, or the nutriment supplied to it, a great variety of materials, but these are seldom stored in such large quantities in animal cells as in those of plants.

In the cells of some kinds of animal textures, particularly that called *Connective Tissue*, we commonly find large quantities of fat formed and accumulated to such a degree in the cell that the protoplasm can be no longer recognized as such. Its remnant is devoted to forming a limiting membrane for the fatty contents, so that the cell is converted into an oil vesicle, and here certainly what may be termed the contents become the most important part of the cell. In various gland cells also, as will be seen hereafter, different substances are made and stored up temporarily in the protoplasm, and these can be seen as bright refracting granules, and are subsequently discharged in the secretion of the gland.

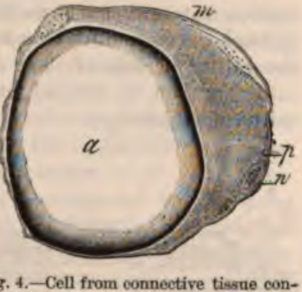


Fig. 4.—Cell from connective tissue containing large fat globule (*a*), and showing protoplasm (*p*), and nucleus (*n*), (*m*) membrane. (Ranvier.)

In other cells again (liver) nutrient material allied to starch may be deposited in considerable quantity, just as starch is stored in certain cells of a plant, but owing to the greater and more constant activity of animals, the amount laid by never attains anything like that found in the store textures of vegetables, where the result of an entire summer's active work is put by as a provision for the next winter, and the fresh burst of energy which follows it in the spring.

But while the above are all more or less temporary contents of cells, we have an example of a permanent deposit in them, viz., Pigment, this substance is formed by the protoplasm in various parts and has a special physiological use. Thus in the cells of the tissue behind the retina—or nerve layer of the eye-ball—the cells are filled with a number of granules composed of a substance very rich in carbon, which when in a sufficiently thick layer is able completely to absorb any light that may fall upon it, thus preventing the reflections that would otherwise occur, and which would interfere with the clearness of sight.

It also occurs in the skin of the negro and other races and in that of the frog and other animals, but in these its function is not fully known.

VARIETIES OF CELLS.—Great varieties of cells are found in the various mature tissues of the higher animals, all of which have passed through the stage of being a simple nucleated mass of protoplasm in the earlier periods of their development and differentiation. All cells may then be divided into two chief types, the indifferent and the differentiated.

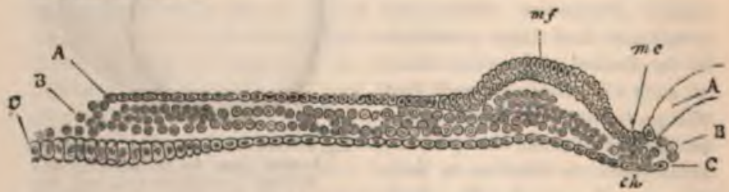


Fig. 5.—Transverse section of Blastoderm, showing the elements in the earlier stage of the development. A, epiblast; B, mesoblast; C, hypoblast.

Under the category of *indifferent cells* may be placed all such as retain the characters of the first embryonic cell and have not acquired any special structure or property by which they can be distinguished from the simplest form. Such cells are the only ones in the early stages of the embryo. In the adult tissues they also occur, having various duties to perform. They are mainly found in the adult in the blood and lymph, and scattered throughout the tissues, and are without a cell wall, and have no special contents to mark their function.

Among the *differentiated cells* we find many special characters, adapting them to certain special duties, for all these cells are modified from the original type and applied to the performance of some special function.

Space prevents even a short enumeration of the varieties of cells met with in the tissues of plants, where they carry on all the active function of the organism as well as form the firm supporting structures.

The differentiation of a cell is accomplished by its own protoplasm, which forms new structural parts and sometimes seems to diminish in quantity until finally an element is produced in which there is no longer any protoplasm recognizable.

We find then matured and differentiated cells which vary—

1. In shape, being spherical, flattened, fusiform, stellate, &c.
2. In size, becoming smaller or larger.
3. In their mode of connection, becoming attached in one way or another to neighbouring cells or structures.

Cells may also be classified according to their function, *e.g.*, Glandular, Nervous, &c., and the greater portion of the following pages will be devoted to the functions of these various forms of cells.

So long as a cell remains in its indifferent stage it possesses the properties of ordinary protoplasm only. But by its further development it acquires special properties not common to all protoplasm. These properties may or may not be accompanied by structural change. Thus the protoplasm of a gland cell differs in little from that of any other cell except in the capabilities of its nutritive changes and its chemical products; while on the other hand, those epithelial cells which form the outer layer of the skin lose completely their protoplasmic characters and are profoundly modified in structure.

MODIFICATIONS OF ORIGINAL CELL—TISSUES.—In the preceding pages the special characters of a single cell have been dwelt on, and it has also been seen that a cell may become changed from its original form in order to fit it more perfectly for some special purpose. But it is necessary to consider this latter fact more fully in order to understand the relation of the various tissues of the adult body to each other.

The first stage in the existence of any organism, from the simplest form of plant to man, is composed of a single cell (in animals called the ovum or egg), which differs in no essential points of structure from an ordinary cell.

There is moreover a class of organisms which never goes beyond this one-celled stage, and the individuals pass their entire life-time in the state of a simple unicellular organism. This group, called *Protista*, though insignificant in point of its size, may vie with the higher plants and animals in number, species, and variety of form, so that they might well be placed in a kingdom by themselves (as has been proposed) apart from the vegetable and animal kingdoms.

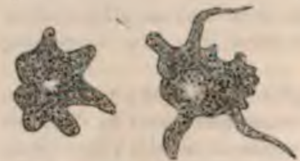


Fig. 6.—Unicellular organism. Small amœba. (Cadiat.)

The group of these organisms which most resemble animals, is called *Protozoa*, and is divided from other animal forms by the manner of development of the ovum of the latter, which differentiates by division into cells. This group is called the *Metazoa*. In the Protozoa the ovum never divides, the animal always remaining a single cell.

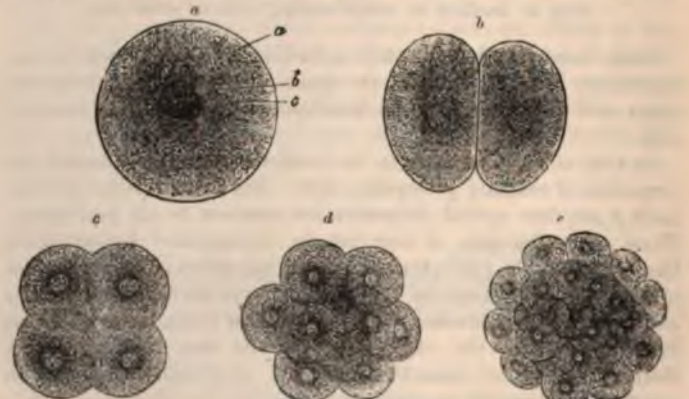


Fig. 7.—Stages in the division of the egg cell (ovum), showing the production of a multiple mass by division. (Gegenbauer.)

On the contrary, the ovum of the Metazoa changes its characters during its development. At first possessing a stage common to both divisions, viz., a single cell, it soon passes through rapid stages of cell proliferation, and is converted into a multiple mass, the mulberry stage or *Morula*.

The cells forming this Morula stage work towards the periphery of the mass, where they tend to arrange themselves in two layers, at the same time forming a cavity in the centre. This is known as the *Gastrula* stage. Following then this cell multiplication or quantitative differentiation, we find a qualitative differentiation of the cells, by which certain groups of cells assume special peculiarities, fitting them for some specific duty.

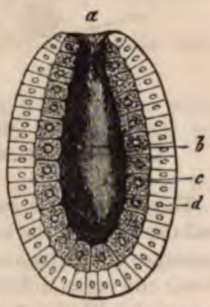


Fig. 8. — Diagram showing the first differentiation of the organism into an external and internal layer. (*a*) Mouth, (*b*) enteric cavity, (*d*) ectoderm, (*c*) endoderm. (Gegenbauer.)

Thus we arrive at the production of special textures and organs such as are met with in the higher animals, and which are necessary for the efficient discharge of the various functions carried on during their lives. The division of the original mass of indifferent cells into two layers of special cells is the first step towards tissue differentiation, and in some animals is the only one arrived at in their entire life history, throughout which they remain a simple sac made up of an external layer, *Ectoderm*, and an internal layer, *Endoderm*.

The groups or layers of cells forming the outer and inner layers of this stage of development, not only form the primitive tissues, but they also represent the first appearance of organs or parts with a specific function. The external or ectodermic layer is the supporting, protecting, motor, and respiratory organ, while the inner or endodermic layer is devoted to a primitive form of digestion, preparing the food for assimilation, and generally presiding over the nutrition of the body.

Although this sac-like (Gastrula) stage is supposed to have formed a step in the life history of nearly all animals, yet it forms a less striking part in the development of the individuals as we ascend the scale, and in the higher animals no such stage has been recognised. In the Vertebrates, the germ cells derived from the ovum are from an early period divided into three distinct layers, owing to the layers which correspond to the Ectoderm and Endoderm of the lower organisms, forming between them a third layer or *Mesoblast*.

From these germinal layers all the organs and tissues of the body are subsequently evolved. In embryological language the three primitive layers are called epi-, meso-, and hypoblast.

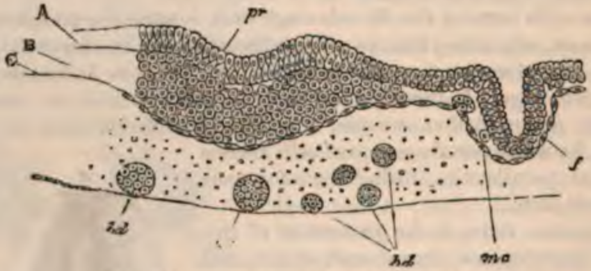


Fig. 9.—Transverse section of blastoderm of chick.

A. Epiblast. B. Mesoblast. C. Hypoblast. *pr*. Primitive groove.

Thus it can be seen that, as we can compare the primitive unicellular state of the lowest animals with the first egg-cell stage of existence of the highest animals, so we can compare all the steps of tissue and organ differentiation as we trace them in the embryo of a mammal, with the steps of elaboration in organic and textural parts that we find in ascending the scale of animal life.

The history then of the development of any mammal from a single cell or egg to the complex adult individual, is strictly analogous with the more protracted history of the evolution of the animal kingdom from the Protista upwards.

It is impossible to separate the differentiation of tissues and organs, or to say which is of older date in the history of animal evolution. Even in unicellular animals, where we have no trace of tissue difference (Paramæcium, Vorticella, there being only one cell), we have a distinct foreshadowing of organ and functional differentiation (vide Chapter III.). And in creatures made of many parts, the same cells have several duties to perform. But when an aggregation of cell units exists, it may be said that a tissue is formed. If these cells be indifferent, that is, have no special characteristic, then the tissue may be called primitive or embryonic. But, as has just been stated, the aggregation of embryonic cells—in the higher forms of life—have special characters from the very first, which mark them off from one another as destined for different functions.

The middle germ layer (mesoblast) is derived from the upper (epiblast) and lower (hypoblast), the part contributed by each being doubtful. From the first the middle layer has distinctive characteristics, and ultimately gives rise to a set of tissues which can always be distinguished from those which originate from the upper and lower layers.

From the inner and outer germ layers are formed several layers of tissues, which, in a more or less perfect degree, retain the activity of the original protoplasm, and hence may be called active tissues. From the middle germinal layer is developed a set of textures, in the majority of which the protoplasmic elements are reduced to a minimum, and are therefore grouped together as supporting tissues.

The tissues formed in the adult may be classified into four groups :—

1. *Epithelial Tissues.* The primitive surface tissues of the outer and inner germ layers, which are variously modified for several distinct duties.
2. *Nerve Tissues.* Springing from the former, are modified for receiving, conducting, controlling, and distributing impressions.
3. *Muscle or Contractile Tissues.* In close relation to both the previous and the next groups.
4. *Connective Tissues* formed only from the middle germ layer. They are much modified in different parts, so as to give shape to the body, and to support and hold the various organs and parts firmly together. They are in fact the materials used in the general body architecture.

EPITHELIAL TISSUE, although the oldest kind of tissue both in the animal series and in the germinal layers, retains the embryonic character of being entirely composed of cells placed in close relationship to each other on the internal and external surfaces of the body. The individual cells, moreover, retain the embryonic character in form and function, being soft rounded masses of protoplasm, only altered in shape by the pressure of their neighbours. The cells which lie next the nutrient vessels of the mesoblast, are endowed with energetic powers of growth and reproduction. As the young cells are produced they take the place of the parent cell, whose future life-history determines the special characters of the different kinds of tissues.

Sometimes the cells are retained, as in the skin, and are arranged in several layers, one over the other. As the cells are conveyed from the deeper layer, where they take their origin, towards the surface, the efforts of the waning nutritive power of the protoplasm are devoted to the manufacture of a tough insoluble substance. The cells thus gradually lose their vital activities, and are converted into horny scales, which form the external protecting skin, and its many modifications that give rise to the different dermal appendages, such as hair, feathers, &c. Instead of a horny substance, the protoplasm may manufacture fat in the bodies of the cells, and the adult cells, being moved on by the young cells arising beneath them, are heaped together as an indefinite mass which passes off as a fatty mixture. In other cases the reproductive activity of the cell is in abeyance, and its remaining nutritive energy is devoted to the manufacture of a material which is poured out of the cell at certain periods. Thus we have another great function performed by the epithelial tissues, namely, that of manufacturing certain materials which, being collected by suitable channels, appear as secretions.

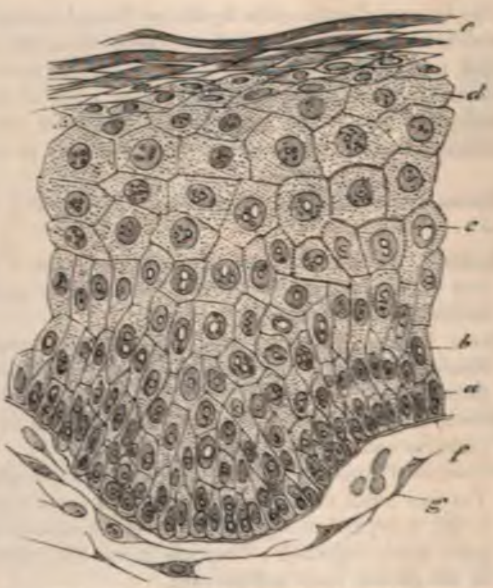


Fig. 10.—Section of the epiderm of the prepuce showing the super-imposed layers of cells of a stratified epithelium. (Cadiat.)

a. Young proliferating cells. *b*—*d.* Cells advancing towards surface. *e.* Flattened cell of horny layer. *f.* Basement membrane. *g.* Connective tissue.

The active elements of glandular tissue are epithelial cells whose nutrition seems to lead to the formation of specific chemical products within their protoplasm. These products pass out commonly as fluids, and form various substances of great importance in the economy. A gland then is simply a special arrangement of epithelial cells, generally lining the sacs or tubes into which the secretion is poured.

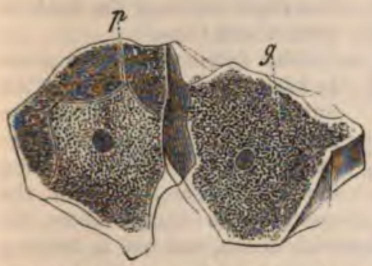


Fig. 11.—Two cells of scaly epithelium from the inside of the cheek. (Ranvier.)

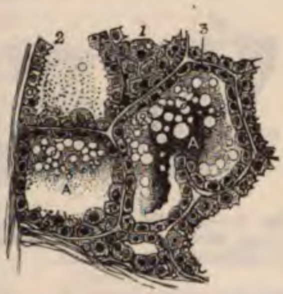


Fig. 12.—Section of milk gland of cat, showing secreting cells containing fat globules, and some secretion in alveoli.

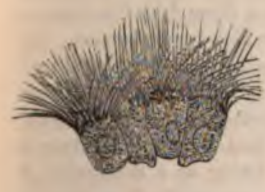


Fig. 13.—Ciliated epithelial cells from the gills of mussel. (Cadiat.)

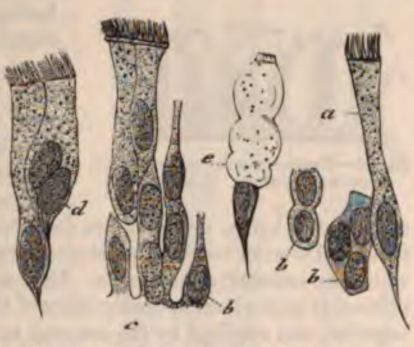


Fig. 14.—Stratified ciliated epithelial cells from the trachea of man. (Cadiat.)

a. Large surface cells, with cilia on surface.
b. Lower cells in earlier stage of development.
e. Cell charged with mucus.

The covering of epithelium is in various places found to be modified in different ways, so as to suit it for the special part in which it is placed. Some tracts are covered with fine moving hair-like processes, called cilia, which give rise to a slight motion of the fluids in contact with them.

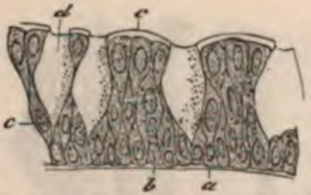


Fig. 15.—Epithelial cells, some of which are filled with mucus (*d*), forming goblet-like cells. (Cadiat.)

Other differences will be given in detail with the description of the duties of the many mucous surfaces. The most striking, and at the same time the most interesting modifications are those in the special sense organs, where the cells are in immediate connection with nerves, and aid in forming the special nerve terminals.*

Nerve Tissue.—The great nervous centres are formed from certain cells of the outer germinal layer, which, in the earliest days of the embryo, dip in as a furrow, and are gradually cut off from the parent tissue by the rapid growth of the middle germ-layer. In looking for special conducting tissue in animals possessing the most simple structure, we find cells which would seem to possess certainly a two-fold, and possibly a three-fold function,—one of which is conduction. In the so-called "neuro-muscular" cells of the hydra, processes are described as found to pass off from them, and to unite beneath the ectoderm with other fibre-like processes, which are eminently contractile. Here we find for the first time a portion of protoplasm specially devoted to acting as a conductor of impulses, and attached by the one end to a contractile fibre, and by the other to a surface (sensory) cell. The intimate relation between the development of nerve and muscle fibres is thus established, and we have the first attempt at a nerve mechanism, viz., a cell capable of receiving impressions, and a fibre capable of transmitting the results of these stimuli. As further differentiation proceeds, each of these parts becomes more distinct from the other, and ultimately the adult

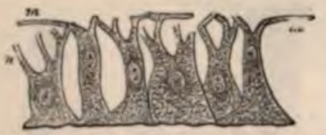


Fig. 16.—Neuro-muscular cells of hydra. *m*. Contractile fibres. (Kleinenberg.)

---

* A fuller account of the Histology of these tissues will be found in the chapters specially devoted to these subjects.

nerve tissue is found to be made up of nerve or *ganglion* cells, nerve fibres, and special nerve endings. The fibres commonly act as lines of communication between two cells: they connect together the numerous cells in the various parts of the brain and spinal cord, or pass between the cells of these central nerve organs and special cells situated throughout the body, which might be called the peripheral nerve organs.

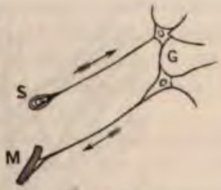


Fig. 17.

S. Sensory receiving organ with attached afferent nerve fibre.
G. Central organs—ganglion cells.
M. Peripheral organ and efferent nerve.

The simplest idea then of a special nerve apparatus is a fibre connecting two cells. The peripheral cell may be a reliving organ (fig. 17, S), from which, when stimulated, impulses are transmitted along the fibre to the central nerve cell, where they give rise to certain impressions, and so we have a sensory nerve apparatus. Or the central nerve cell may be the receiving agent, getting stimuli from its central neighbours, and transmitting impulses to a peripheral nerve terminal, by which the energy is, as it were, handed over to a muscle (M) or gland, and so we have a simple motor or secretory apparatus. Where the effect of a stimulus can be definitely traced from one nerve cell to another, and from thence by a second fibre to a third cell, the impulse is said to be reflected by the second cell to the third. And there we have what is called a reflex act.

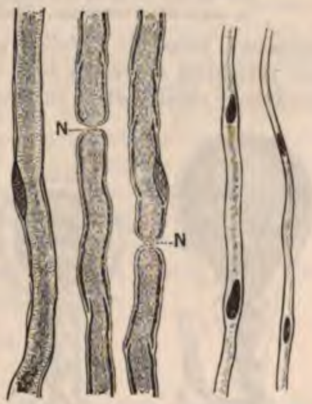


Fig. 18.—Three medullated nerve fibres, the medullary sheath of which is stained dark with osmic acid. N, Nodes of Ranvier.
Two non-medullated nerve fibres, with nuclei in the primitive sheath.

The essential part of a nerve fibre is a kind of protoplasmic band, in which the finest fibrilla or thread-like marking can be made out with the aid of reagents and a powerful microscope. This is called the *axis-cylinder*. In some nerve fibres (mostly in the brain and spinal cord) the axis-cylinder is naked, and even, a single fibrilla may so pass from one cell to another in the brain matter. In other parts the axis cylinder is generally covered by a thin membrane, called the *primitive sheath*, or with a soft oil-like substance, called the *medullary sheath*, or, as is commonly the case in all peripheral nerves, by both. The primitive sheath encloses the medullary sheath, which surrounds the axis-cylinder.

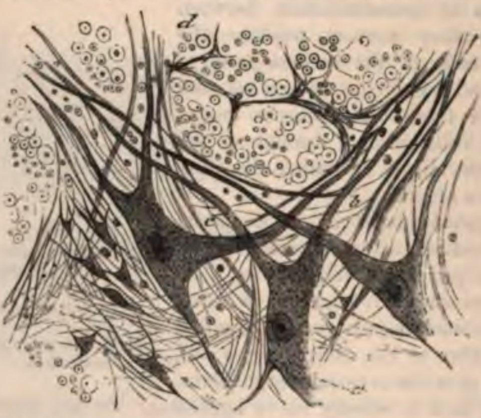


Fig. 19.—Multipolar cells from the anterior grey column of the spinal cord of the dog-fish (*a*) lying in a texture of fibrils; (*b*) prolongation from cells; (*c*) nerve-fibres cut across. (Cadiat.)

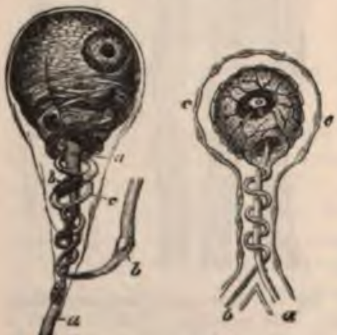


Fig. 20.—Ganglion cells of frog, showing straight and spiral fibres. (After Beale and Arnold).

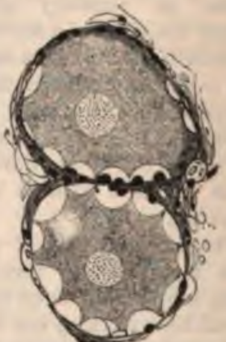


Fig. 21.—Cells from the sympathetic ganglion of a cat. The delicate protoplasm has shrivelled here and there from the cell wall.

These fibres are made of peculiarly modified cells, which are, however, so elongated as not to be very easily recognised as such in adult tissue.

The nerve or ganglion cells vary extremely in general form and size. The commonest in the nerve centres are large bodies with a clear well-defined single nucleus, and distinct nucleolus; they commonly have two or more processes, which are connected by nerve fibres to other cells, and to the axis-cylinder of nerves. This latter does not branch as the other processes sometimes do, and when it can be traced, appears to enter the protoplasm, running towards the nucleus.

The peripheral nerve cells are generally much modified, and often small compared with those in the centres. Besides the cells in the sporadic ganglia, which are large rounded corpuscles with but few processes—there are many other bodies connected with the peripheral nerves which cannot be called ganglion corpuscles. They are, however, nevertheless nerve cells.

MUSCLES OR CONTRACTILE TISSUES.—When changes take place in protoplasm adapting it specially for contraction, it is termed muscle tissue. The large masses of this tissue attached to the skeleton so as to move its various parts, form the flesh of the higher animals. Muscle tissue is, almost invariably, connected with nerve tissue, and acts in response to stimuli communicated from the nerves. In some of the lower animals the two tissues are so intimately related that it is not easy to separate them, and the development of both progresses equally as we ascend the scale of animal life. They are nearly related in their origin, or even spring from the same primitive tissue. In fact, as has already been mentioned (*vide* p. 20), they form but one structure in some of the more simple and less differentiated animals. The neuro-muscular tissue which is formed from the outer layer of the embryo, is the forerunner of the muscles as well as of the nerves of the embryo of the higher animals.

In the higher animals and man muscle tissue consists of two distinct kinds of textures, commonly spoken of as—

a. Smooth or non-striated muscle.
b. Striated muscle.

In the smooth muscle the individual elements present all the characters of a cell, but very much elongated and flattened, and contain a single long nucleus. They contract very slowly and persistently and require a comparatively long time for the nerve influence to affect them, so that an obvious interval exists between the moment of their stimulation and their contraction. They are therefore commonly found in the internal organs and in situations where gradual and lasting contractions are required. They receive their nervous supply generally from the sympathetic system, and perform their duty without our being conscious of their activity or being able to control it by our will.

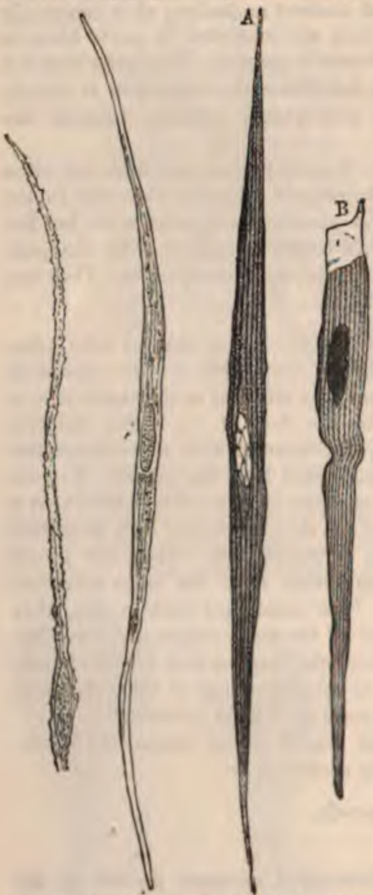


Fig. 22.—Cells of smooth muscle tissue from the intestinal tract of rabbit. (Ranvier.)

A. and B.—Muscle cells in which differentiation of the protoplasm can be well seen. (Schäfer.)

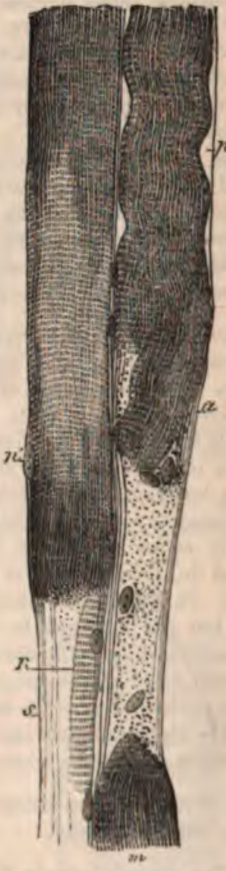


Fig. 23.—Two fibres of striated muscle, in which the contractile substance (m) has been ruptured and separated from the sarcolemma (a) and (s); (p) space under sarcolemma. (Ranvier.)

Striated muscle tissue is made up of cylindrical fibres of such length that both extremities cannot be brought into the field of the microscope at the same time. Their exact relation to cells is not so easily made out as in smooth muscle, and doubtless varies in different muscles. Sometimes the fibres are made up of single cells, and in other cases they are formed by the permanent fusion of several cell elements which never differentiate into separate elements, owing to the imperfect division of the cells, but make up one mass, the multiple nuclei of which alone make its mode of origin apparent. The contractile substance is made up of two kinds of material, one of which refracts light singly, while the other is doubly refracting. These are ranged alternately across the fibre, making the transverse markings or striæ from which it gets its name. This striated material is quite soft and is encased in a thin homogeneous elastic sheath called *sarcolemma*, which keeps the fibre in its normal shape.

This form of muscle may be considered the widest departure from the primitive protoplasmic type imparting to it contractility. It moves with wonderful rapidity, contracting almost the instant its nerve is stimulated. It forms the great mass of the quick-acting skeletal muscles, being attached to the bones by bands composed of a form of fibrous connective tissue, which form the tendons and fasciæ. Muscles made of striated tissue are commonly under the control of the will, and hence are frequently spoken of as voluntary muscles, but this term is misleading, for many striated muscles are not governed by voluntary control.

THE CONNECTIVE TISSUE group, coming exclusively from the middle germinal layer, exhibits very great varieties of form. Its cells differ much from the epithelial cells both in their character and their relations, and particularly in the adult tissues.

Under the heading Connective Tissues are generally classed all those which support the frame and hold together the various other tissues and organs. They are—

1. Mucous and retiform connective tissue.
2. White and yellow fibrous tissue.
3. Cartilage.
4. Bone—as well as certain modifications of these types.

The cells of all these tissues have the property of manufacturing some material which however does not generally enclose them as a cell wall, but remains between the cells and forms the intercellular substance. The younger the tissue the greater is the proportion of its cell constituents, and the older the issue the greater will be found the preponderance of the intercellular substance.

Mucous Tissue.—In certain parts of the embryo and in some of the lower animals a kind of connective tissue is found in which there is but little intercellular substance, the mass of the tissue being thus made up of cells. This cellular connective tissue never forms an important texture in the adult man, but is interesting as the probable tissue from which all the connective tissues are formed in the embryo, and as occurring in abnormal growths or tumours.

The first step in differentiation is the secretion of a large quantity of soft homogeneous, semi-gelatinous or fluid material like the mucus secreted by epithelium. In this the cells lie, either free or united by long protoplasmic processes. This is the *mucous tissue* common in the lower animals, in textures of the embryo in the adult and in pathological growths of the connective tissue type. The processes uniting the cells may not be present, and the cells may be reduced to a minimum, as occurs in the vitreous humour of the eye. But more commonly the soft gelatinous substance is reduced in amount, and the processes connecting the cells are converted into a dense network of delicate threads to form the retiform tissue of lymphoid structures.

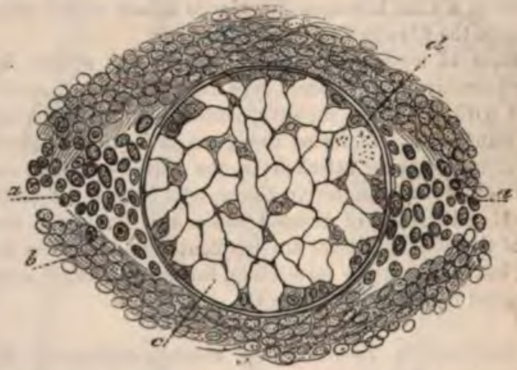


Fig. 24.—Transverse section of the chorda dorsalis and neighbouring substance. *a*, cartilage cells; *b*, cell of the middle layer of embryo; *c*, mucous tissue; *d*, boundary of chorda. (Cadiat.)

Fibrous Tissue.—The cells may become further differentiated and fibrillated. When the thickness of the cell processes is great, and their fibrillation well marked, the cells appear to devote all their reproductive energy to the formation of this fibrillated substance which ultimately forms the great bulk of the tissue, while the cells become gradually and proportionately fewer in number. In this case only sufficient of the mucous substance generally remains to cement the fibrils together into bundles. A few of the cells, however, remain between the bundles of fibrils to preside over the nutrition of the tissue. Thus is formed the non-elastic or white fibrous tissue of tendon.

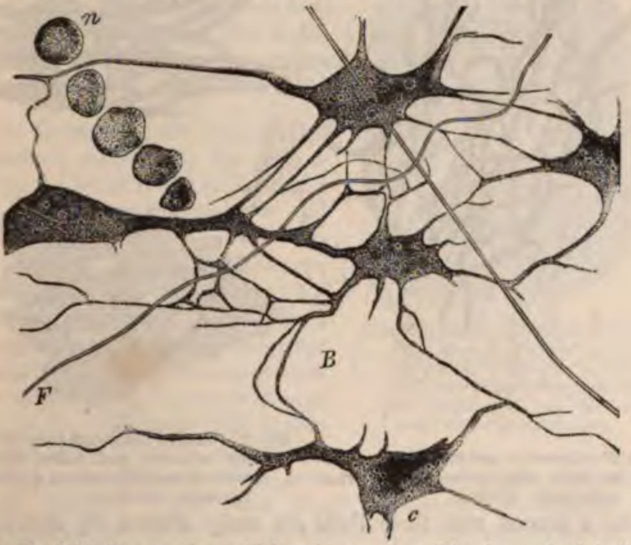


Fig. 25.—Cells of mucous tissue with branching processes (B) and a couple of elastic fibres (F). (Ranvier.)

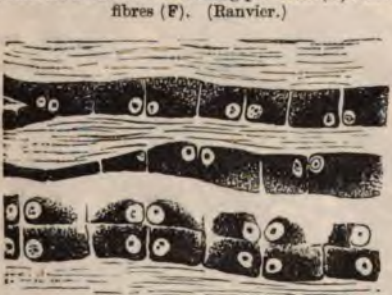


Fig. 26.—Portion of tendon from the tail of a young rat, stained with gold chloride, showing arrangement of flattened cells on bundles of fibrils. (After Klein.)

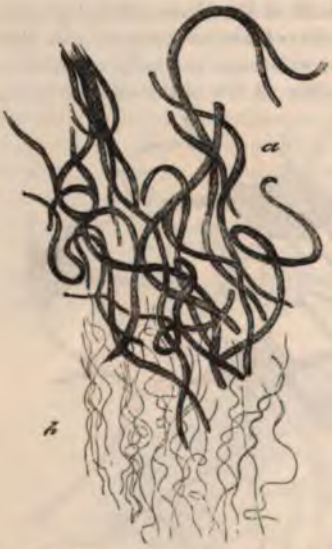


Fig. 27.—Coarse (*a*) and fine (*b*) yellow elastic fibres after treatment with strong acetic acid. (Cadiat.)

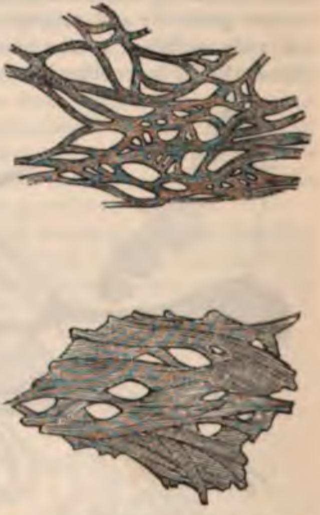


Fig. 28.—Elastic membrane from inner coat of aorta, and, below, meshwork of elastic fibres from a yellow ligament. (Cadiat.)

As a general rule these fibrils are easily affected by chemical re-agents. Weak acids cause them to swell up and become indistinct. Baryta water affects the cement and renders them easily separable. They swell and dissolve in boiling water yielding gelatine, which forms a jelly on cooling.

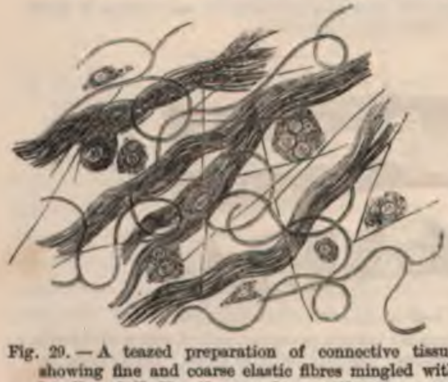


Fig. 29.—A teazed preparation of connective tissue showing fine and coarse elastic fibres mingled with bundles of fibrillar tissue and connective tissue corpuscles.

In some parts of the body, however, a different kind or intercellular substance is formed, which is highly elastic, does not give gelatine on boiling, and is not affected by weak acids or alkalies. This is spoken of as *Yellow elastic tissue.* It is sometimes found alone forming an elastic band or ligament, but more commonly mingled with fibrillar tissue to form the common connecting medium which lies under the skin and between the various other textures.

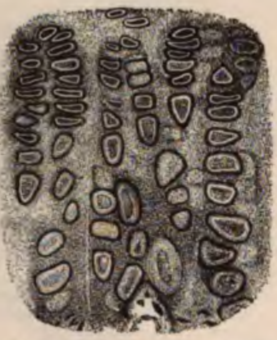


Fig. 30.—Section of hyaline cartilage from the end of a growing bone, showing a decrease in the intercellular substance compared with the number of cell elements, which are arranged in rows.

In Cartilage the intercellular substance secreted by the cells is hard, and forms in the earlier stages of its development cases or cell walls for the cells. These cases subsequently increase in thickness, and become fused together into a homogeneous intercellular substance, where ultimately the capsules belonging to the different cells can no longer be distinguished from one another, so that in the adult tissue there is seen to be a tough matrix of intercellular substance, in which the cells are scattered, apparently occupying small cavities. These cells, which are the remote offspring of those which formed the tissue permanently, preside over its nutrition.

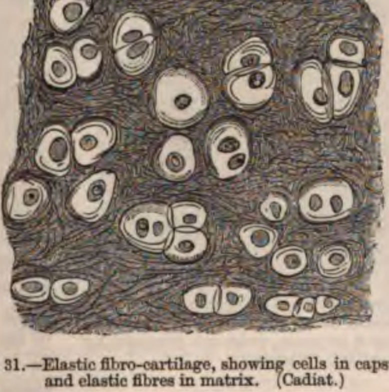


Fig. 31.—Elastic fibro-cartilage, showing cells in capsules and elastic fibres in matrix. (Cadiat.)

The intercellular substance, which is quite homogeneous in common hyaline cartilage, is sometimes modified so as to resemble fibrous tissue, sometimes the fibrillar, and sometimes the elastic form being produced. (Figs. 31 and 32.)

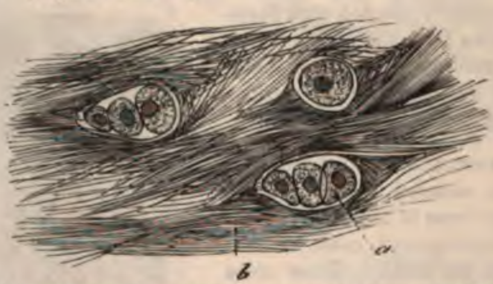


Fig. 32.—White fibro-cartilage, showing cells (*a*) in capsules and fibrillar matrix (*b*). (Cadiat.)

Bone is probably the most advanced differentiation of the connective tissue group. The intercellular substance is characterised by containing a great quantity of earthy or inorganic matter, which gives the tissue its enormous strength. It is, moreover, everywhere traversed by the processes of the cells lying in little canals (canaliculi), which connect the spaces (lacunæ) in which the protoplasmic bone cells sojourn.

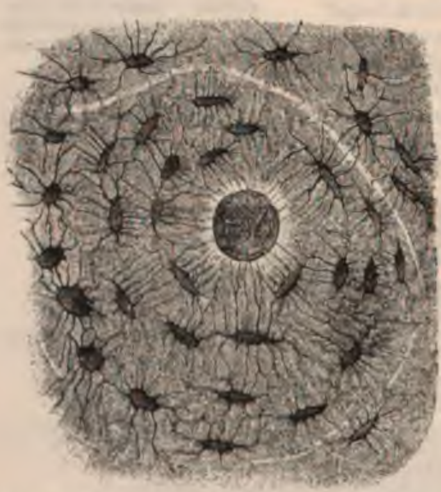


Fig. 33.—Transverse section of a system of Havers, showing Haversian canal in centre, with bone cells arranged around it in *lacunæ*, which are connected by the delicate *canaliculi*. (Cadiat.)

In the formation of bone from fibrous or cartilaginous tissue the original intercellular substance disappears, and a set of cells with new

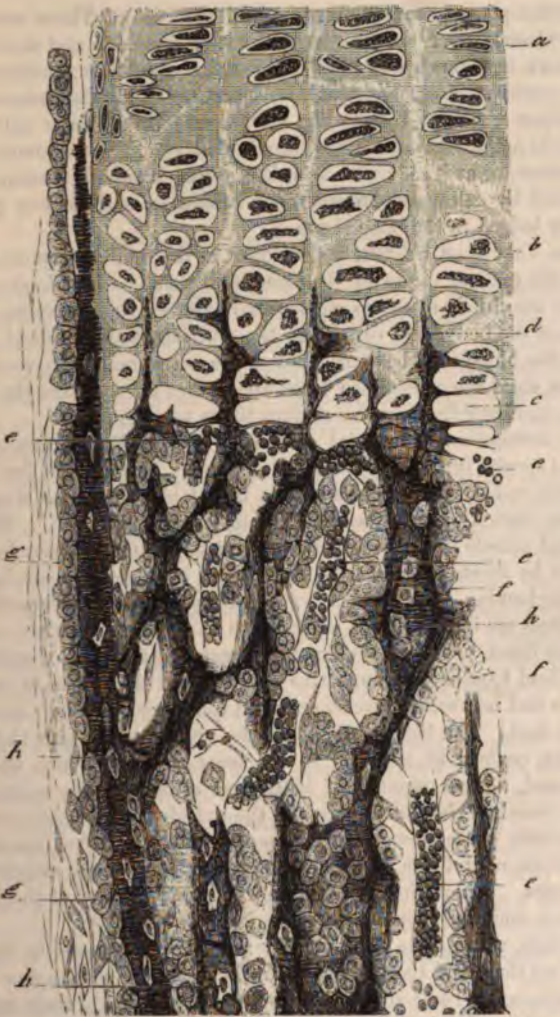


Fig. 34.—Section through ossifying cartilage and newly-formed bone. (Cadiat.)

a. Developing cartilage cells.
b. Degenerating cartilage cells.
c. Cell space, empty.
d. Spiculæ of calcareous deposit.
e. Blood corpuscles.
f. Osteoblasts.
g. Ditto of periosteum.
h. Bone cells.

formative powers come upon the field (Fig. 34). These new cells (osteoblasts) cover the growing surface of the bone and secrete and lay down in layers a new kind of intercellular substance, which is the bone matrix. Here and there at wonderfully regular intervals an osteoblast ceases to secrete the calcareous intercellular substance, while its neighbours continue formative activity. Consequently, this osteoblast, or as it may now be called young bone cell, becomes surrounded by calcareous intercellular substance, and is thus permanently lodged in the bone tissue.

The VASCULAR SYSTEM is developed in the middle germinal layer with the earliest stages of the connective tissue. The blood vessels, which are chiefly made up of connective tissues, soon traverse all the parts of the body, and distribute the nutrient fluid or blood. And even the blood may be considered as an outcome of the connective tissues, since the cells of the blood are at first formed from the mesoblast, and later from the connective tissue corpuscles.

An arrangement of special cells, such as epithelial or muscle cells, with a special function, constitutes an organ. However, in the higher animals and man an organ is almost invariably a complex structure, having various tissues entering into its construction. Thus a skeletal muscle is made up of a quantity of muscle fibres held together by sheets of connective tissue, and attached to bones by connecting bands. It is further traversed by many blood vessels, and the fibres are in immediate relation to certain nerves which terminate in them. The various secreting organs are made up of epithelial cells, held together by connective tissue and in close relation to blood vessels and nerves, and are so arranged that they pour their secretion into a duct. The bones, which are the organs which give the body support, contain in addition to the bone tissue of which they are composed, a great quantity of indifferent cells, fat cells, nerves and blood vessels. They are covered on the outside with a tough vascular coat, which gives them strength, assists their nutritive repair and reproduction, and acts as a point of attachment for the muscles and ligaments. Where the bones are in immediate relation at the joints, they are commonly tipped with cartilage.

If, then, we analyse anatomically the architecture of the human body, we shall find that it is made up of a number of complex parts, each adapted to some special function, and composed of such an association of the simple tissues as the special part demands.

The general arrangement of these organs and their modes of action will be discussed in a future chapter.

CHAPTER III.

CHEMICAL BASIS OF THE BODY.

It seems natural to commence the description of the molecular changes that take place in the various tissues and organs of the body, with a brief account of the chemical composition of the most characteristic substances found in animal textures, because none of the mysterious processes of cell life, or tissue activity, can be satisfactorily studied without familiarity with the more common terms occurring in physiological chemistry.

The chapter on this subject here introduced, is intended rather to give the medical student a general view of the chemical composition and characters of those substances most frequently met with in the chemical changes specially connected with animal life, than to supply a complete or systematic account of the relationships of the chemical bases of the body, for which reference must be made to more advanced text books, or treatises on the special subject of physiological chemistry. This review must moreover be inadequate in the case of many bodies, but they will be again referred to when speaking of the function with which they are associated.

It has already been stated that of the sixty-three elements known to chemists, a comparatively small number form the great bulk of the animal body, although traces of many are constantly present. Thus, we shall see that four elements, namely, (1) oxygen, (2) carbon, (3) hydrogen, (4) nitrogen, are present in large proportions in every tissue, and together make up about 97 per cent. of the body; and sulphur, phosphorus, chlorine, fluorine, silicon, potassium, sodium, magnesium, calcium and iron, are indispensable to the economy, and are widely distributed, but are found in comparatively minute quantities. Occasionally traces of zinc, lead, copper, lithium, and other minerals may be detected, but these must be regarded rather as accidental than indispensable ingredients.

The attempt to investigate the composition of a living tissue by chemical analysis, must cause its death, and thus alter the arrangements of its constituents, so that its true molecular constitution when alive, cannot be determined.

We know that the composition of all living textures is extremely complicated, every one being made up of a great number of components, most of which contain many chemical elements associated together in very complex proportions.

But as has already been pointed out, the complexity of their chemical constitution is not so wonderful as another fact which sounds paradoxical, that, in order to preserve their elaborate composition, they must constantly undergo a change or renewal, which is necessary for, and forms the one essential characteristic of, their life. In fact, their complexity and instability is such, that they require constant reconstruction to make up for the changes inseparable from their functional activity.

Their chemical constituents are easily and permanently dissociated, and the various components are themselves readily decomposed, generally uniting with oxygen to form more stable compounds.

The investigation of the chemical changes, known as assimilation, forms a great part of physiological study, and therefore will occupy many chapters of this book. Here we can only call attention to the chief characteristic substances to be found in the animal body, as the result of the primary dissociation or death of the textures, and briefly enumerate the products of their further decomposition as obtained by the analysis of the different substances.

The tissues of the higher animals present a greater variety of substances, materially differing in chemical composition; they have, however, all been made from protoplasm, and contain a proportion of some substance forming a leading chemical constituent of protoplasm. Every living tissue contains either protoplasm or a derivative of it, and the special characters of each tissue depend upon the greater development of some one of these substances.

It is of little use to classify the numerous chemical constituents found in the animal body, in such a systematic manner as to satisfy the rules of modern chemistry, because their classification from a strictly chemical point of view, does not set forth their physiological importance or express in any way the relation they bear to the vital phenomena of organisms.

The following enumeration of the chief chemical ingredients found in the tissues has regard to their physiological dignity as well as to their chemical construction, and will thus it is hoped assist the student to distinguish the different groups, and give him a better idea of their vital relationships, than a more strictly systematic classification.

A. NITROGENOUS.

I. Complex bodies forming the active portions of all tissues—Plasmata. *E.g.*, protoplasm, blood-plasma.
II. Bodies entering into the formation of, and which can easily be obtained by analysis of Group I., Albumins. *E.g.*, serum-albumin.
III. Bodies the outcome of differentiation, manufactured in the tissues by Group I., Albuminoids. *E.g.*, gelatin, &c.
IV. Bodies containing nitrogen, being intermediate, bye, or effete products of tissue manufacture. *E.g.*, lecithin, urea, &c.

B. NON-NITROGENOUS.

V. Carbohydrates in which the hydrogen and oxygen exist in the proportion found in water. *E.g.*, starch and sugar.
VI. Hydrocarbons containing oxygen in less proportions than the above. *E.g.*, fats.
VII. Salts.
VIII. Water.

CLASS A. NITROGENOUS.

Group I. PLASMATA.

Under this group may be placed a great variety of materials which must be acknowledged to exist in the living tissues as exalted chemical compounds, of whose chemical constitution, however, we are ignorant, since it is altered by the death of the tissue.

There are some exceedingly unstable associations of albuminous bodies with other substances, and they at once break up into their more stable constituents, dead albumins, fats, salts, &c., as soon as they are deprived of the opportunities of chemical interchange and assimilation which are necessary for their life.

Although we can only theorise as to the real chemical constitution of such substances, we must believe that they really exist in the living tissues as chemical compounds, and, moreover, as chemical compounds endowed with special properties which impart the specific activity of their textures, whose molecular motions in fact are the essence of the life of the tissues.

Protoplasm: By far the most widely spread and important of these is the soft jelly-like substance, Protoplasm. This is the really active part of growing textures of all organisms, whether animal or vegetable, and forms the entire mass of those intermediate forms of life, the protista, which are now generally regarded as the original fountain head of life on the globe.

This material commonly exists in small independent masses (cells), in which we can watch all the manifestations of life, assimilation, growth, motion, &c., taking place. We must assume that this substance is a definite chemical compound; and, further, since the living phenomena are exhibited only so long as it preserves its chemical integrity, we may conclude that its manifestations of life depend upon the sustentation of a special chemical equilibrium. Not only is this equilibrium destroyed by any attempt to ascertain the chemical composition of protoplasm by analysis, but even for its preservation the protoplasm must be surrounded by those circumstances which are known to be necessary for life, viz., moisture, warmth, and suitable nutritive material, or its chemical destruction must be warded off by a degree of cold that checks its chemical activity.

If the chemical integrity of protoplasm be destroyed and its death produced, many new substances appear, amongst which are representatives of each of the great chemical groups found in the animal tissues. Thus, besides water and inorganic salts we get from protoplasm carbohydrates represented by glycogen, lecithin, and other fats, and several albuminous bodies, which will be described in the groups to which they belong. In addition to these, protoplasm often contains some foreign bodies which have come from without, and special ingredients of its own manufacture, such as oil, pigment, starch, and chlorophyll.

Blood-plasma: There is another body in living blood which must be included in this group, as it undoubtedly has a much more complex constitution than any of the individual albuminous bodies, presently to be described, which can be obtained from it. This is proved by the following facts: first, its death is accompanied by a series of chemical changes, viz., disappearance of free oxygen, diminution of alkalinity, and a rise in temperature, and secondly, that several albuminous bodies appear which were not present as such in the living plasma.

The spontaneous decomposition of separated blood-plasma may be delayed by cold; at freezing point the chemical processes are thus held in check. During life the exalted constitution of the plasma is sustained by certain chemical interchanges which go on between it and its surroundings. This question will be more fully discussed when the coagulation of the blood is described.

Muscle-plasma: Likewise, as will be found in the chapter on Muscles, there exists in the soft, contractile part of striated muscles a plasma which at its death spontaneously breaks up into several distinct albuminous bodies [and forms a coagulum. These changes are accompanied by acidity of reaction, the disappearance of oxygen and an elevation of temperature, showing that distinct chemical change is taking place.

Oxy-hæmoglobin, the colouring matter of the blood, should be included here amongst the important chemical bodies more complex than the albumins. This singular body can be broken up into a globulin and a colouring matter *hæmatin* containing iron. It differs from all other bodies of a similarly complex nature from the fact that it readily crystallizes, and also in the very remarkable manner in which it combines with oxygen, and again yields it up.

Group II. ALBUMINOUS BODIES.

It is difficult to say how far these bodies exist as such in the living organism, but they can be obtained from nearly all parts, particularly those which contain active protoplasm, and after its death they can be detected in abundance. As may be seen, by testing for their presence in living protoplasm, the addition of any chemical re-agent or treatment causes its death, so that although albumins appear in the test-tube, this cannot be accepted as proof that they would have answered to the tests before the protoplasm was changed by its death.

They do not occur normally in any secretion except those substances which tend to nourish the adult body, and to form and nourish the offspring, viz., the ovum, semen, and milk. No satisfactory formula has been suggested to express their chemical composition, but the average per-centage of the elements they contain is remarkably alike in all members of the group. This may be said to be in round numbers as follows :—

Oxygen	21 per cent.
Hydrogen	7 „
Nitrogen	16 „
Carbon	53 „
Sulphur	1 „

They are amorphous, of varying solubility, and with one exception indiffusible in water.

As far as we know at present, albumins cannot be constructed *de novo* in the animal body, but must be supplied in one form or another as part of the food. Albumins are therefore always the outcome of the activity of vegetable life.

They can be recognised by the following tests :—

1. Strong nitric acid gives a pale yellow colour to strong solutions or solid albumin, which turns to deep orange when ammonia is added (*Xanthoproteic test*).
2. Millon's Re-agent (acid solution of proto-nitrate of mercury) gives a white precipitate which soon turns yellow, changing to rosy-red on prolonged boiling, or after standing for some days.
3. Solution of caustic soda and a drop of cupric sulphate solution give a violet colour to the liquid.
4. Acetic acid and boiling give a white precipitate.
5. Acetic acid and potassium ferro-cyanide give a flocculent white precipitate.
6. Acetic acid and equal volumes of sodium sulphate solution give a precipitate on boiling.
7 With sugar and sulphuric acid they become violet.
8. Crystals of picric acid added to their solutions dissolve and at the same time cause bead-like local coagulations.

CLASSIFICATION OF ALBUMINS.

Under the head of the albuminous bodies we find several classes which differ from each other in slight but very important points. The first class may be called

A. *Albumins Proper, or Native Albumins.*

They consist of :

1. *Egg-Albumin*, which does not occur in the ordinary tissues of the animal, can be procured by filtration from the white of an egg. It makes a clear or slightly opalescent solution in water, from which it is precipitated by mercuric chloride, silver nitrate, lead acetate, and alcohol. It is coagulated by heat, strong nitric and hydrochloric acids, or prolonged exposure to alcohol and ether.

2. *Serum-Albumin*, on the other hand, is one of the chief forms of albumin found in the nutrient fluids.

It differs from egg-albumin in—

(*a*.) Not coagulating with ether.
(*b*.) The precipitate obtained by strong hydrochloric acid being readily redissolved by excess of the acid.
(*c*.) Coagulum being more readily soluble in nitric acid.
(*d*.) Its specific rotatory power being 56°, while that of egg-albumin is 35·5°.

(*e*.) If introduced into the circulation, it is not eliminated with the urine as is egg-albumin.

B. *Globulins.*

Associated with the last during the life of the tissues we find another class of albumins, namely, the globulins, which do not dissolve in pure water, but are more or less soluble in a solution of common salt. These may be divided as follows :—

1. *Globulin* (crystalline) occurs in many tissues, but is usually obtained from an extract of the crystalline lens made by triturating it with fine sand in a weak solution of common salt, and then passing a current of carbon dioxide through the solution. The globulin falls, being easily precipitable from its saline solution by very weak acid. This form of globulin does not cause coagulation on its being added to a serous fluid, and in this respect differs from the next members of this division.

2. *Paraglobulin* (*fibrinoplastin*) can be obtained by passing through diluted serum a brisk stream of carbon dioxide. When a fluid containing paraglobulin is added to a serous transudation, it causes coagulation of the fluid giving rise to fibrin.

3. *Fibrinogen*, a viscous precipitate got from serous fluids or blood in the same way as the last, but with greater dilution and more prolonged use of carbon dioxide. It is similar in its characters to the last, but coagulates at a lower temperature (55° C.) (paraglobulin coagulating at 60°—70° C.). On its addition to defibrinated blood, or a fluid containing paraglobulin, it forms a coagulum.

4. *Myosin*, obtained from dead muscle, being the soft jelly-like clot formed during *rigor mortis* from the dying muscle plasma. It is not so soluble as globulin, for it requires a stronger solution of salt to dissolve it, and is precipitated from its saline solution by solid salt or by dilution. It is coagulated at 60° C.

5. *Vitellin*, a white granular proteid obtained from the yolk of egg. It is very soluble in 10 per cent. saline solution, from which it can be precipitated by extreme dilution, but not by saturation with salt. It coagulates between 70° and 80° C.

C. *Derived Albumins* (*Albuminates*).

1. *Acid-Albumin* (Syntonin) can be made from any of the preceding by the slow action of a weak acid ; or by the addition of strong acetic or hydrochloric acids to native albumin, such as exists in white of egg, and dissolving the jelly, thus formed, in water. It is only

soluble in weak acids—exact neutralisation precipitating it. With the least excess of alkali the precipitate redissolves, becoming changed into alkali-albumin.

So long as it is dissolved in weak acid it will not coagulate on boiling, but it coagulates and becomes incapable of re-solution if heated while precipitated by neutralisation.

2. *Alkali-Albumin.*—Similar to the last, but produced by the action of either weak alkalies and dilute solutions, or strong solution of potash on white of egg. Its general behaviour is the same as the above—but as it differs in composition, containing no sulphur—it can therefore be distinguished by the absence of the brown colouration which appears on heating acid-albumin with caustic potash and lead acetate.

3. *Casein* is the proteid existing in milk, and resembles alkali-albumin in its reactions. It can be precipitated from milk by *rennet*, or acetic acid in excess, but not by exact neutralisation, owing to the presence of potassium phosphate.

D. *Fibrin.*

A solid filamentous body, the result of chemical changes accompanying the death of the blood-plasma, during which the so-called fibrin generators are set free. It swells in weak hydrochloric acid, but does not dissolve while cold. If heated to 60° C. in acid, it changes to acid-albumin and dissolves. By 10 per cent. neutral saline solutions, a substance like a globulin may be extracted from it. If heated, it assumes the characters of a coagulated proteid.

E. *Coagulated Albumin.*

If any of the above be heated to 70° C. (except acid and alkali albumin, which must first be precipitated by neutralisation) they coagulate and become extremely insoluble and lose their former characters. They are but very slightly acted on by weak acids, even when warmed. Strong acids dissolve them, but this solution is associated with a destructive change. They are, however, readily converted by the digestive ferments and juices into peptones, and thus dissolved.

F. *Peptone.*

This substance is formed by the action of the digestive ferments from any of the above albumins, in the stomach by pepsin in the presence of dilute acid, and in the small intestines by trypsin in the presence of dilute alkali. This change renders them more soluble and diffusible, and thus enables them to pass out of the alimentary canal into the system, and makes them more suited to take part in the nourishment of the body.

The leading characteristics of peptone may be thus enumerated :—

1. Very ready solubility in hot or cold water, acids or alkalies.
2. Not coagulable by heat.
3. They are precipitated by alcohol but not changed to the coagulated form.
4. They diffuse readily through animal membrane.
5. They are not precipitated by sulphate of copper, chloride of iron, or ferro-cyanide of potassium and acetic acid.
6. They are precipitated by iodine, chlorine, tannin, chloride of mercury, and the nitrates of silver and mercury.
7. Caustic potash and a trace of sulphate of copper added to their solutions give a red colour which deepens to violet if too much of the copper salt be used.

The formation of peptones is a gradual process having many intermediate steps, in the earlier stages of which, precipitates are formed by ferro-cyanide of potassium and acetic acid. (*Vide* Chaps. VIII. and IX. and on Chemistry of Digestion, pp. 116 and 124.)

Group III. ALBUMINOIDS.

These are the outcome of nutritive modification of protoplasm, and may be said to be directly manufactured by that substance, and to be specially adapted to meet the requirements of certain textures differing widely in function. They are allied to one another and to the last group by—(a) their per centage composition [*] ; (b) containing nitrogen ; (c) being amorphous colloids. They differ from albuminous bodies in—(a) their solubility ; (b) their behaviour to heat, acids, alkalies and the digestive fluids ; and (c) their value as food-stuffs.

1. *Mucin* is the characteristic ingredient of the mucus manufactured by epithelial cells, and is also found in connective tissue (abundantly

---

[*] The following Table gives the composition of the principal albuminoids and albumin :—

	Gelatin.	Elastin.	Chondrin.	Mucin.	Keratin.	Albumin.
C	50 °/.	55 °/.	47 °/.	50 °/.	51 °/.	51—54 °/.
H	7	7	6	7	6	6—7
N	18	17	14	10	17	15—17
O	23	20	31	33	21	20—23
S	0·5		0·6		3	2—2·3

in that of the fœtus) and in some pathological growths. It gives a peculiar thick ropy consistence to the fluid containing it, enabling it to be drawn into threads. It is precipitated by mineral acids, alum, and alcohol, and the precipitate swells in water and is re-dissolved in excess of the acid. With acetic acid a precipitate is formed which does not re-dissolve in an excess of the acid. When boiled with sulphuric acid it yields leucin and tyrosin.

2. *Chondrin* is obtained by the prolonged boiling in water of slices of cartilage cleared of the perichondrium. On cooling, this solution forms a jelly. The jelly dissolves easily in hot water or alkalies, and can be precipitated by acetic or weak mineral acids, alum or acetate of lead. It gives only leucin on boiling with sulphuric acid.

3. *Gelatin* is produced by boiling fibrous connective tissues, such as ligaments, tendons, the true skin and bones in water. On cooling, the fluid forms a jelly, which can be dried to a colourless brittle body which swells in cold water and dissolves on being heated. It is not precipitated by acetic acid, but yields precipitates with chloride of mercury or tannin, which latter is seen in making leather. On boiling with sulphuric acid it yields glycin and leucin but no tyrosin.

4. *Elastin* is obtained from yellow elastic tissue by boiling with caustic alkalies. It is little affected by boiling water, strong acetic acid, or weak alkalies, but dissolves in concentrated sulphuric acid. It is precipitated by tannin, and yields leucin when boiled with sulphuric acid.

5. *Keratin* exists in the epidermic appendages (hair, horn, nails, &c.). It is like the albuminous bodies in containing a considerable quantity of sulphur, but differs from them and the other albuminoids in general properties. It is soluble in alkalies, swells in strong acetic acid, gives the xanthoproteic reaction, and is extremely insoluble in the digestive juices.

Group IV. PRODUCTS OF TISSUE CHANGE.

Intermediate or bye products.

These are, no doubt, protoplasmic manufactures destined for some useful purpose, but they do not long exist in their original form, being often broken up into other compounds they are re-absorbed, or pass away with the fæces. These bodies are found in the various secretions. Most of them, however, can be better described with the function of the gland which forms the secretion in which they occur.

Attention must here be drawn however to certain complex bodies existing in the bile. Some complex nitrogenous substances and the monatomic alcohol, cholesterin, will also be now mentioned. But the reader must remember that chemically they are not connected with the other bodies the description of which immediately follows theirs, namely, the effete products.

Bile Salts.—Two acids exist in the bile united with soda to form soluble soap-like salts. They may be recognised by the purple violet colour produced by cane sugar and sulphuric acid at a temperature of about 70° C. (Pettenkofer's reaction).

Taurocholic Acid, $C_{26}H_{45}NSO_7$, is most plentiful in the bile of carnivora and man, where it occurs combined with soda. It is decomposed by prolonged boiling with water into taurin and cholic acid, thus :—

$$\overset{\text{Taurocholic Acid.}}{C_{26}H_{45}NSO_7} + H_2O = \overset{\text{Taurin.}}{C_2H_7NSO_3} + \overset{\text{Cholic Acid.}}{C_{24}H_{40}O_5}.$$

Glycocholic Acid, $C_{26}H_{43}NO_6$, found in the bile of herbivora and man. It crystallises in fine white glistening needles. It exists as the glycocholate of soda in the bile. By boiling with weak acid it yields glycin and cholic acid.

$$\overset{\text{Glycocholic Acid.}}{C_{26}H_{43}NO_6} + H_2O = \overset{\text{Glycin.}}{C_2NH_5O_2} + \overset{\text{Cholic Acid.}}{C_{24}H_{40}O_5}.$$

In the bile certain matters also exist to which the colour is due, the principal being *bilirubin* in man and carnivora, and *biliverdin* in herbivora. They are probably derived from the colouring matter of the blood. They can be recognised by treating the solution with nitric acid which is coloured with red fumes, when a play of colours ending in a dull purple is seen.

Lecithin, $C_{44}H_{90}NPO_9$, is a complex nitrogenous fat found in most tissues and fluids of the body, particularly in the nerve tissues and yolk of egg. It is an interesting product of decomposition of the constituents of the brain, which is related in constitution to the neutral fats, and it may be regarded as an acid glycerine ether. It is easily decomposed when heated with baryta water, splitting into glycerin, phosphoric acid, neurin, and barium stearate.

Another body called *Cerebrin*, not containing any phosphorus and of doubtful composition, can be obtained from brain substance, and is also found in nerve fibres and pus corpuscles. It is a light colourless powder which swells in water.

Protagon, $C_{160}H_{308}N_5PO_{35}$, is by some supposed to be the chief constituent of brain substance, and by others said to be a mixture of the last two bodies.

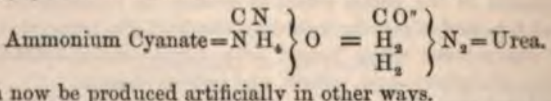
Neurin (Cholin), $C_5H_{13}NO_2$, is an oily liquid only found in the body as a product of the decomposition of lecithin, but it has been obtained synthetically.

Cholesterin, $C_{26}H_{44}O$, exists throughout the body where active tissue change is going on, particularly the nervous centres. It is a monatomic alcohol, and is the only one existing free in the body. It may be obtained from gall-stones, some of which consist entirely of cholesterin. It may occasionally be found in a crystallised form in any of the fluids of the body normal or pathological, but it only seems to be an effete product, nearly all that produced in the body being discharged along with the effete portions of the bile. It may be recognised by the shape of the crystals, which are rhombic plates, in which one corner is generally deficient.

Effete Products.

These, as has been stated before, are generally the outcome of the active chemical changes necessary for the growth and vitality of the living protoplasm, and are for the most part soon eliminated by the excretory glands, so that but small quantities of them can be found in the active tissues where they are produced.

Urea, $CO(NH_2)_2$, is the most important constituent of the urine of mammalia, but not of that of birds or reptiles. Traces of it may be found in the fluids and tissues of the body. It is readily soluble in water and alcohol, and forms crystals when its solution is concentrated. It decomposes when treated with some strong acids or alkalies, taking up water and yielding CO_2 and NH_3, and with nitrous acid gives $CO_2 + N + H_2O$. It was the first of the so-called "organic" compounds to be made artificially, being obtained in 1828 by mixing watery solutions of cyanate of potassium and sulphate of ammonium, evaporating to dryness and extracting with alcohol, or in short by heating cyanate of ammonia with which it is isomeric.



$$\text{Ammonium Cyanate} = \left.\begin{matrix}CN\\NH_4\end{matrix}\right\}O = \left.\begin{matrix}CO''\\H_2\\H_2\end{matrix}\right\}N_2 = \text{Urea.}$$

It can now be produced artificially in other ways.

It has also been considered to be a diamide of carbonic acid ($CO(OH)_2$), the two atoms of hydroxyl being replaced by two atoms of amidogen, NH_2, thus—($CO(NH_2)_2$). In the presence of septic agencies, in a watery solution, urea takes up two atoms of water and is converted into carbonate of ammonium—

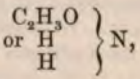
$$CO(NH_2)_2 + 2H_2O = CO(ONH_4)_2.$$

The so-called alkaline fermentation of urine depends upon this change. The reader is referred to the Chapter on Excretions, p. 329, where more complete information is given.

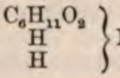
Kreatin, $C_4H_9N_3O_2$, occurs in muscle and many other textures. It may be converted into kreatinin by the action of acids by simple dehydration. It can also be split up into sarcosin and urea.

Kreatinin, $C_4H_7N_3O$, is a dehydrated form of kreatin, which is a normal constituent of urine. In watery solutions it is slowly converted into kreatin.

Allantoin, $C_4H_6N_4O_3$, found in the allantoic fluid and the urine of the fœtus and pregnant women. It is crystallisable, and is converted into urea and allantoic acid by oxidation.

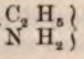


Glycin (*Glycocoll* or *Glycocine*) $C_2H_2(NH_2)O{\cdot}OH$, or $\left.\begin{array}{c}C_2H_3O\\ H\\ H\end{array}\right\}N$, is regarded as amido-acetic acid. It does not occur free in the body, but enters into the composition of the bile acids and hippuric acid. It is soluble in water.



Leucin, $C_6H_{10}(NH_2)O{\cdot}OH$, or $\left.\begin{array}{c}C_6H_{11}O_2\\ H\\ H\end{array}\right\}N$, amido-caproic acid, is found in the secretion of the pancreas and some other glands. It is one of the principal products of the decomposition of albuminous bodies, from which it can be obtained by boiling with sulphuric acid.

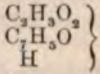
Tyrosin, $C_9H_{11}NO_3$, though belonging to a distinct chemical series (aromatic), is only found in company with leucin in the decomposition of albuminous bodies, and normally in the pancreatic secretion.



Taurin, $C_2H_7NO_3S$, or $\left.\begin{array}{cc}C_2 & H_5\\ N & H_2\end{array}\right\}SO_3$, is a constituent of one of the bile acids, and is also found in muscle-juice. It may be regarded as amido-ethyl-sulphonic acid.

Uric Acid, $C_5H_4N_4O_3$ (dibasic), is found in large quantities in the excrement of birds and reptiles, but in a small and variable quantity in the urine of man. Traces have been found in many tissues, in some of which large quantities accumulate as the result of pathological processes (gout). It forms salts which are much less soluble in cold than in hot water, and make the common sediment in urine. The acid salts are less soluble than the neutral. The common test for uric acid consists of slowly evaporating the substance to dryness with a little nitric acid, and to the residue adding ammonia when a bright purple colour is produced (murexide test). Uric acid is supposed to be a step in the production of urea, which is one of the results of its oxidation in the presence of acids, thus :—

$$\underset{\text{Uric Acid.}}{C_5H_4N_4O_3} + H_2O + O = \underset{\text{Alloxan.}}{C_4H_2N_2O_4} + \underset{\text{Urea.}}{CO(NH_2)_2}.$$



Hippuric Acid, $C_9H_9NO_3$, or $\left.\begin{matrix} C_2H_3O_2 \\ C_7H_5O \\ H \end{matrix}\right\} N$, occurs in considerable quantities in the urine of the horse and herbivora generally. It is found but very sparingly in man's urine, but it appears in large quantities after benzoic acid and some other medicaments have been taken. In constitution it is an amido-acetic acid in which one atom of the hydrogen is replaced by the radical benzoyl (C_7H_5O). In the body it is combined with bases, and is formed out of benzoic acid and glycin (amido-acetic acid) (*vide* p. 332), thus—

$$\underset{\text{Glycin.}}{C_2H_2(NH_2)O{\cdot}OH} + \underset{\text{Benzoic Acid.}}{C_7H_6O_2} = \underset{\text{Hippuric Acid.}}{C_2H(C_7H_5O)(NH_2)O{\cdot}OH} + \underset{\text{Water.}}{H_2O}.$$

By heating or putrefaction it is resolved into these constituents.

Indol, C_8H_7N, is produced in the intestinal canal by the putrefactive changes brought about by septic agencies during pancreatic digestion. It gives an odour to the fæces and a red colour with nitrous acid.

Indican, a peculiar substance sometimes found in the urine and sweat. With oxidising agents it yields indigo blue. By this fact it is easily recognised. An equal volume of hydrochloric acid and a very small quantity of calcium hypochlorite (bleaching-lime) is added, and the indigo which is formed can then be dissolved and separated by agitation with chloroform.

CLASS B. NON-NITROGENOUS.

Group V. CARBOHYDRATES.

Carbohydrates (general formula, $C_nH_{2n}O_n$) are bodies in which the hydrogen and oxygen exist in the same proportion as in water, the carbon being variable. The following examples of this group are met with in the textures of the body :—

Grape Sugar (*Dextrose*), $C_6H_{12}O_6$, occurs in minute quantities in the blood, chyle, and lymph. It forms crystals which readily dissolve in their own weight of water. The watery solution has a dextro-rotatory power on the ray of polarised light. When mixed with yeast, the fungus (*Saccharomyces cerevisiæ*) of the yeast causes *alcoholic fermentation* of the sugar, whereby alcohol and carbon-dioxide are formed.

Dextrose. Alcohol.

$$C_6H_{12}O_6 = 2\ C_2H_6O + 2\ CO_2$$

Moderate heat (25° C.) aids the process, and cold below 5° C. checks it ; an excess of either sugar or alcohol stops it.

The presence of casein or other proteid material, when decomposing, gives rise to *lactic fermentation*, producing first lactic acid, then butyric and carbon-dioxide and hydrogen.

Dextrose. Lactic Acid. Butyric Acid.

$$C_6H_{12}O_6 = 2\ C_3H_6O_3 = C_4H_8O_2 + 2\ CO_2 + H_4$$

Milk Sugar (*Lactose*), $C_{12}H_{22}O_{11} + H_2O$, isomeric with cane sugar (sucrose).—It is the characteristic sugar found in milk. It is not so soluble as dextrose, and does not undergo direct alcoholic fermentation, but under the influence of certain organisms it readily gives rise to lactic acid by lactic fermentation in the same way as dextrose. (See Milk.)

Inosit, $C_6H_{12}O_6 + 2\ H_2O$, is an isomer of grape sugar, which is incapable of undergoing alcoholic fermentation. It is crystallisable, and easily soluble in water. It has no effect on the polarised ray. It is found in the muscles, and also in the lungs, spleen, liver, and brain.

Glycogen, $C_6H_{10}O_5$, a body like dextrin, first found in the liver. It gives an opalescent solution in water, and is readily converted into dextrose by an amylolytic ferment, or weak acids. It has a strong dextro-rotatory power. It can be found in most rapidly growing tissues. (See Glycogenic Function of the Liver, p. 307.)

Group VI. HYDROCARBONS.

These bodies have the same elements in their composition, but the hydrogen and oxygen have variable proportions—not that of water. Fats are found in large masses in some tissues, and also as fine particles suspended in many of the fluids. The fat of adipose tissue in man is a mixture of olein, palmitin, and stearin, which are commonly spoken of as the neutral fats.

The first is liquid and the last two solid at normal temperatures, and the varying consistence of the fat of different animals depends upon the relative proportions of the more solid or liquid fats.

Fats are soluble in ether and chloroform, but quite insoluble in water. When agitated in water containing an albuminous body, or an alkaline carbonate in solution, fluid fat is broken up into small particles, which remain suspended in the liquid so as to form an opaque milky emulsion.

Chemically, they are regarded as ethers derived from the triatomic alcohol glycerine, $C_3H_5(OH)_3$, by replacing the hydrogen atoms of the OH group by the oxidised radicals of the fatty acids: thus—

$$\begin{array}{ccccccc} \text{Glycerine} & + & \text{Palmitic Acid} & = & \text{Tripalmitin} & + & \text{Water.} \\ C_3H_5(OH)_3 & + & 3\ (C_{16}H_{32}O_2) & = & C_3H_5O_3\ (C_{16}H_{31}O)_3 & + & 3\ H_2O. \end{array}$$

Under the influence of certain ferments they separate into glycerine and the fatty acid, taking up the necessary elements of water.

When the neutral fats are boiled with alkaline solutions they are similarly decomposed, and uniting with the elements of water, form glycerine and fatty acids. The glycerine is thus set free, but the fatty acid combines with the alkaline metal to form a kind of soluble *soap*. An insoluble soap may be obtained by substituting lead or lime, &c., for the alkali.

This splitting up of the neutral fats, stearin, palmitin, and olein into sodium stearate, palmitate, or oleate goes on during digestion, and is said to be useful in aiding the absorption of fatty matters.

INORGANIC BODIES.

Water (H_2O) is present in nearly all tissues in larger proportion than any other compound, making up about 70 per cent. of the entire body-weight. The amount in each texture varies, and thus the different tissues have widely different consistence.

Water is introduced into the body in all kinds of drink, and a large quantity is also taken with our solid food. It is highly probable, that in the chemical changes which take place in the tissues, some water is formed by the oxidisation of the hydrogen of the more complex substances.

In the economy it acts as the universal solvent in the fluids of the body, and as the agent by means of which the chemical changes of the various organs are enabled to be accomplished.

The water leaves the body by the lungs as vapour, and by the skin, kidney, and many other glands, as the fluid in which their secretions are dissolved.

Inorganic acids occur either combined to form salts, in which condition we find several in the body, (sulphuric, phosphoric, silicic), or uncombined. In the latter state we have only two, viz :—

Hydrochloric Acid, H Cl, which is manufactured by the mucous membrane of the stomach, and takes an important part in gastric digestion.

Carbonic Acid Gas, CO_2, exists in most of the fluids of the body, having been absorbed by them from the tissues during their combustion. The venous blood contains a considerable quantity, which is got rid of during the passage of the blood through the lungs. It is distinctly a waste product, that must be constantly eliminated from the body (see Respiration).

A large number of salts occur in the tissues, generally in small quantity, in solution. In the teeth and in bone tissue salts exist in the solid form, and in much greater proportion than in any of the soft parts. Most of the salts are introduced into the economy with the food, but some, doubtless, are formed in the body itself. Our knowledge of the exact position occupied by the salts in the textures is very incomplete, as their amount is only estimated from the ash of the tissue which remains after ignition, by which process they become altered, so that it is impossible to say what are the exact salts that are present in the body. They doubtless form chemical combinations with the complex organic compounds, which we do not understand, and probably have important functions to perform, such as rendering certain materials (globulins) soluble, or otherwise facilitating tissue change. The salts pass out of the body in many secretions, notably in the urine, where they have great influence on the elimination of urea, and therefore form a most important constituent of that secretion.

Common Salt (Sodium Chloride), NaCl, is the most widely spread, and is present in greater quantity than any other salt in all fluids and tissues, except in bones, teeth, red blood corpuscles, and red muscle.

Potassium Chloride commonly accompanies sodium chloride in small quantity. In the red blood corpuscles, and in muscle it occurs in greater amount than the sodium salt, while in the blood plasma but little is found in comparison with the soda salts, and any excess seems to act as a poison to the heart.

Carbonates and phosphates of calcium, sodium, potassium, and magnesium occur in small quantities in most tissues. The earthy part of bone is chiefly composed of calcium and magnesium phosphate and calcium carbonate, together with some calcium fluoride.

Sulphates of sodium and potassium, probably formed in the body from the oxidisation of the sulphur in the complex proteid materials, occur in most tissues, and are removed from the body by the kidneys.

Finally we find two of the elements free in the textures. Of these *Oxygen* plays by far the most important part. It is widely distributed among the fluids of the body, from which it can be removed by reducing the pressure of the oxygen of the atmosphere by means of an air-pump. Oxygen is introduced into the body by the lungs, where the blood takes it from the air. In the blood only a small quantity of that which can be removed by the air-pump is really free, the remainder is chemically combined with the colouring matter of the blood. It is absolutely necessary for life, as it alone can enable the chemical changes of the tissues, which are mostly oxidisations, to go on. It is, in fact, the element necessary for the slow combustion which takes place in the nutrient material after its assimilation.

Nitrogen also occurs in the blood, but in insignificant quantity. It is absorbed from the atmosphere as the blood passes through the lungs. So far as we know, it has no physiological importance in the body.

CHAPTER IV.

THE VITAL CHARACTERS OF ORGANISMS.

THE manifestation of so-called vital phenomena in man forms the subject-matter of the following chapters, and some kind of explanatory definition of the vital characters of the simpler organisms will be useful in preparing the beginner's mind for the more intricate questions in human physiology. This, with the foregoing short account of the chemical and structural peculiarities of animals, will complete a rough outline of the general character of organisms.

Protoplasm has already been referred to as the material capable of showing "vital phenomena," the most obvious and striking of which are its movements.

Besides the common molecular or Brownian movement of the granules of protoplasm—which may be seen in most cases where fine granules are suspended in a less dense medium—protoplasm can perform motions of different kinds which must be regarded as distinctly vital in character. This movement may be said to be of three different kinds, according to the results produced, viz. :—(1.) The production of internal currents. (2.) Changes in form. (3.) Locomotion. In reality the two latter are dependent on the first.

The occurrence of currents from one part of a portion of protoplasm to another can be well seen in vegetable cells, when the cell wall restricts the more obvious change in form or place. Thus in the cells forming the hair on the stamens of *Tradescantia Virginica* the various currents can be seen in the layers of protoplasm which line the cell wall.

The granular particles course along in varying but definite directions, passing one another like foot-passengers in a crowded street. The first and most obvious result of this is, that the various parts of the substance are constantly brought into contact with one another, and thus the products of any chemical changes taking place at any given part of the cell body are rapidly distributed over the entire mass of the protoplasm.

If there be no definite cell wall—as in naked vegetable spores and amœboid forms of animal life—to restrict or direct the current of protoplasm, it flows out in various directions in budlike processes, which appear at various parts of the protoplasmic mass, so as to cause a constant change in the form of the cell. These outstretched processes sometimes flow together and unite completely, often enclosing some of the medium in which the creature is suspended, or catching some foreign particle floating near them.

The flowing out of these *pseudopodia* commonly takes place for some little time persistently from one side of the cell; and the body of the cell, as it were, has to follow the protrusion of the processes in such a manner that in a little time definite change in position or movement in a certain direction occurs; thus the unit of protoplasm may be said to perform definite progression or locomotion. All these movements may be seen in the white blood corpuscle of a cold-blooded animal, such as a frog, and still more easily in the unicellular being known as amœba.

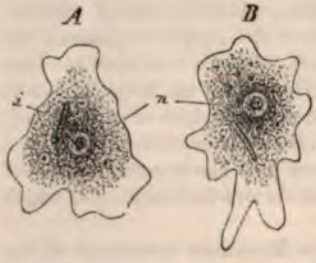


Fig. 35.—An amœba figured at two different moments during movement, showing a clear outer layer and a more granular central portion. (n) Nucleus; (i) Ingested food. (Gegenbauer.)

Various influences may be seen to affect the rate of movements, and probably influence at the same time the other activities of the protoplasm. Foremost among these must be named:—(1.) *Temperature.* If a protoplasmic unit which is observed to be motile be gently warmed, the movements become more and more active as the temperature is raised, until at a certain point, about 35°—42° C., a spasm occurs, resulting in the withdrawal of the pseudopodia; soon after which the cell assumes a spherical shape. If the heat be carefully abstracted by the gentle and short application of cold, the protoplasm may be made to recover and again commence its movements. If, on the other hand, cold be applied to moving protoplasm, the motions become less and less active, and commonly cease at a temperature about or a little over 0° C. (2.) *Mechanical irritation* also produces a marked effect on the movements of protoplasm. This may be well seen in the behaviour of a protoplasmic cell of frog's blood under the microscope. It is spherical when first mounted, owing to the rough treatment it goes through while being placed on the glass slide and covered; shortly its movements become obvious by its change in form, which may again be checked by a sudden motion of the cover-glass. (3.) *Electric shocks* given by means of a rapidly-broken induced current cause spasm of the protoplasm, the cell becoming spherical. (4.) *Chemical stimuli* also have a marked effect; carbonic acid causing the movements to cease, and a supply of oxygen making it active. The movements and other activities of protoplasm are, during life, frequently modified and controlled by nerve influence, as will appear in the following pages; this may readily be seen in the stellate pigment cells of the frog's skin, which can be made to contract into spheres by the stimulation of the nerves leading to the part.

The motions of protoplasm are thus seen to be greatly affected by external influences, but the most careful observer cannot find physical explanations of the various movements which have been described. It is necessary, therefore, to ascribe this power of motion to some property inherent in the protoplasm, and hence the movements are called *automatic*. We are unable to follow the chemical processes upon which the activities of the protoplasm depend, and therefore we call them *vital actions;* but we must assume that these so-called vital properties depend on certain decompositions in the chemical constitution of the protoplasm. We know that some chemical changes do take place, as we can estimate the products which indicate a kind of combustion; but we know little or nothing of the details of the chemical process.

From the foregoing description of the manner in which protoplasm responds to external stimuli, it may be gathered that it is capable of appreciating impressions from without; indeed, we may say, *it can feel.* We can only judge of the sensitiveness of any creature by the manner in which it responds to stimuli, and we may therefore conclude that the smallest particle of living protoplasm is endowed with definite sensitiveness: this must be noted as one of the most striking properties of protoplasm.

Every particle of living protoplasm has the power of assimilation. Taking into its structure any nutrient matters it meets with, by flowing around them in the way mentioned, it brings them into direct contact with different parts of the protoplasmic substance. This nutrition of the form-units gives rise to growth, and finally leads to their reproduction, and these facts will be more closely examined when speaking of their relation to cell life.

When a certain size has been attained, the cell does not increase any more, but tends to bring forth a cell unit similar to itself. This is spoken of as the *reproduction* of cells.

Different kinds of cell reproduction have been observed, which are all, however, modifications of the same general plan. The first is that by the formation of a *bud* from the side of the parent cell ; this bud then increases in size, and finally separates from the parent and becomes a separate individual. This process, which is called *gemmation*, can readily be seen in all its stages in growing yeast, where the torula cells have various-sized buds growing from them. If the budlike protrusion be large, nearly equal in size to the cell itself, the process receives the name of fission, or division. In well marked typical fission the parent cell divides into two parts of equal size, each of which becomes a perfect individual. Various gradations may be traced between the two processes, so that it is difficult to draw any very distinct line between budding and fission. The budding and fission may be multiple ; many buds and several units, products of division, may remain together, and form what is called a colony. When this multiple budding or division takes place, so that the new units are included within the body of the parent cell, then the process is called *endogenous reproduction* or spore formation. As in the gradations between budding and fission, so it is difficult to draw a hard and fast line between what may be called multiple fission and spore formation.

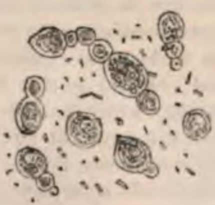


Fig. 36.—Cells of the yeast-plant in process of budding, between which are some bacteria.

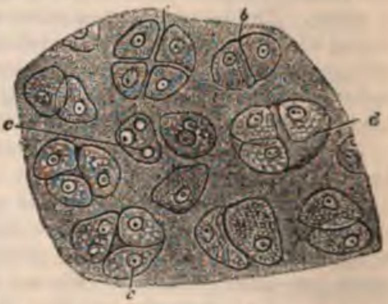


Fig. 37.—Cartilage from young animal showing the division of the cells (*a*, *b*, *c*, *d*).

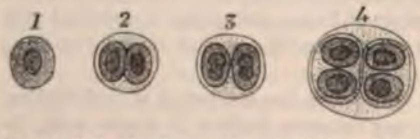


Fig. 38.—Cells of a fungus (*Glæocapsa*) showing different stage (1—4) of endogenous division. (After Sachs.)

In tracing the stages of development of the highly differentiated cells of some tissues, we have to pass through a series of changes which form a cycle that may well be called the life-time of the cell. The duration of this cycle varies greatly in different individual cells. Some cells are very short-lived, being destroyed in the act of secretion; others probably endure for the entire life of the animal. The life-history of all cells begins with the stage when it is composed entirely of indifferent protoplasm, in which various modifications are subsequently produced. Let us take as an example a cell of the outer skin or *cuticle*, and examine its life-history. The cuticle is made up of numerous layers of cells laid one on the other, and the surface cells are constantly being rubbed or worn off. We find that these cells have their origin from the cells of the deepest layer, which is next to the supply of nutriment. This layer is made of soft protoplasmic units, with certain specific inherited characteristics no doubt, but to all appearances the same as the motile sentient growing protoplasm of an indifferent cell. By a process of fission or budding constantly going on in this deepest layer of these cells, new protoplasmic units are produced. These become distinct individuals, and occupy the position of the parent cell, which having produced offspring, is moved one place nearer the surface, away from the supply of food. The new cell in time gives rise to offspring, and having attained reproductive maturity, is in turn moved onward towards the surface. The result of this is that its supply of nutrition diminishes,

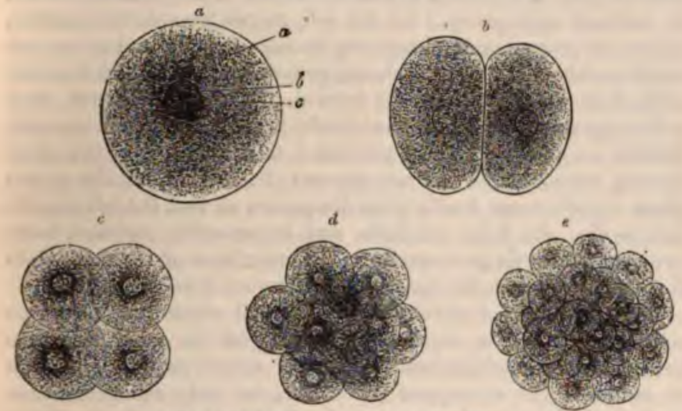


Fig. 39.—Division of egg-cell. (Gegenbauer.)

the evidences of reproductive activity disappear, and at a certain point all signs of protoplasmic life are lost. But on its way from the seat of its origin to the surface, it makes use of its limited supply of nutrition for the purpose of manufacturing a special kind of material which, if present at all, only occurs in the minutest traces in ordinary protoplasm. As the cell moves towards the surface, it loses its protoplasmic characters, becomes tougher and drier, and finally nothing but the special horny material remains. Thus from the birth of the cell, its energies are devoted, first to its own growth, then to the reproduction of its like, and finally to the formation of a material fitted to act as a mechanical protection to the surface of the skin. Having manufactured a certain amount of this material, the protoplasm dwindles, and finally quite disappears, so that the cell may be said to die. Its horny insoluble and impermeable skeleton, however, has yet to do good service in the outer layer of the skin while it is passing to reach the surface, and in its turn is rubbed off.

It has already been stated that the material which forms all active cells, protoplasm, is capable of carrying on the many functions required for the independent existence of simple creatures. It will be found in the subsequent pages that, not only can protoplasm perform all the activities necessary for the life-history of unicellular organisms, but that it can also work out all the functions of the most complex animals. Indeed, the cells which accomplish the most elaborate functions in man, are but protoplasm more or less modified for the special purpose to be attained.

The different functions of an independent unicellular organism can be much more completely watched than the changes which take place in any of the cells of the higher animals, both on account of the greater size of the former, and the more obvious character of the changes taking place in them. The student is therefore earnestly advised to spend a few moments in contemplating the operations which go on in some simple organisms, whose life is not complicated by structural or functional elaboration, before attempting to solve the difficult question of the mechanism of man's life.

The lowest forms of living creatures that we are acquainted with (*micrococcus* and *bacterium*), are placed among the fungi in the vegetable kingdom. On account of their extremely minute size—being hardly visible as spherical or elongated specks with a powerful microscope—we can say but little about their structure. They appear to be translucent and homogeneous.

Since we use the term protoplasm to mean the material of which the active part of the simplest forms of living beings are composed, we must assume that bacteria are small particles of that material, but the characters commonly attributed to protoplasm cannot be detected in the minute glistening mass which makes up their body.

They are so certain to appear in a couple of days in organic infusions, or in any fluid prone to putrefaction, and they multiply with such astounding rapidity, that they have been supposed by some to develop spontaneously. But this is now known not to be a fact. Bacteria do not appear without progenitors, any more than any other form of living thing. They float lifeless and dry in multitudes through our atmosphere, and adhere to all substances to which the air has free access. However, the moment they light upon a suitable soil, they burst into prodigious activity, at first forming masses or colonies, which may be seen as a jelly-like scum on the fluid. Such a soil is supplied by any organic substance capable of spontaneous decomposition, for which process, as is well known, the great requirements for life, moisture and warmth, to a certain degree are necessary. Vast varieties of these organisms are now known. They differ slightly in shape, in their habitat, and in their properties. Some are obviously composed of two distinct layers, some are provided with a fine hair-like process, by the lash-like motions of which they move rapidly in a definite direction.

They are known to be inseparable from putrefactive changes in organic materials, in fact without them no putrefaction can go on, since this process is but the product of their living activity. Intense heat kills them, too great cold or dryness checks their activity and stops putrefaction. When an organic substance is absolutely protected from their presence by exclusion of the air, &c., no putrefaction occurs, even though it be prone to spontaneous decomposition, and be placed under favourable circumstances as to warmth and moisture.

Bacteria would not deserve so much notice here were it not for the remarkable influence they have on the higher forms of life. We do not know that they are necessary for any of the more important processes that normally go on in the human body, though they are constantly present in the intestinal tract, and are inseparable from at least one change taking place there that may be regarded as physiological. It is their relation to the diseased state that makes a knowledge of these creatures imperative to medical men.

So long as the tissue of a higher animal is healthy and well nourished, bacteria cannot thrive in immediate contact with it. They can only exist in the intestine, &c., because there they find accumulations of lifeless fluids which offer them a suitable nidus. Active living tissues have antiseptic power, *i.e.* are able to destroy bacteria, and it is only owing to this bactericide power of our textures, that we can with immunity breathe into our lungs the atmospheric air, and swallow multitudes of these organisms. But for it every wound would become putrid, every breath would admit deadly germs to our blood. But when the vitality of the part or of the body generally is lowered, the vital activity of the tissue may fall below that of the bacteria, and their victory is signalled by unwonted and often fatal changes. Morbid fluids allowed to accumulate in the textures facilitate the growth of bacteria, and give rise to various grades of "wound-infection." But if all accumulations be avoided, the bacteria brought into relation with the living tissue can only irritate it, and cause general fever and local suffering to the patient. They cannot propagate in live tissue as in lifeless fluids. As a rule, the injurious effect of bacteria is in inverse proportion to the vital power of the textures which they invade. This is seen in many cases familiar to the physician and the surgeon. For instance, even the bronchial mucous membrane may be unable to resist the attacks of the atmospheric organisms. A person whose vital powers are probably already low from repeated debauch, falling asleep in the open air after excessive intemperance, and being exposed to the reducing chill of night, may become so lowered in vital activity, that putrefactive changes may begin in his lung tissue. Indeed this is not an uncommon history in the beginning of gangrene of the lung.

We next come to forms of fungus, which set up a process very like putrefaction, such as the yeast plant, *Torula cerevisia*, which causes alcoholic fermentation in sugar solutions. In the torula an external case containing protoplasm may readily be seen, and multiplication of the cells goes on rapidly by a process of budding. Torulæ, however, like bacteria, though called vegetables, have not the power of assimilating as ordinary green plants do, but require nutriment to be supplied to them which already contains organic or complex compounds. Structurally but little different from torula is a one-celled plant, the green protococcus, which, like a higher plant, can build up its texture from the simplest food-stuffs, and carry on its functions. It consists of a case made of cellulose, within which lies a mass of protoplasm with a nucleus. The protoplasm is commonly coloured green by a peculiar substance called chlorophyll. We shall see presently that it is to protoplasm containing chlorophyll, that plants owe all their most characteristic and wonderful properties; viz., the property of assimilating so as to construct complex carbon compounds out of simple inorganic materials.

The smallest and simplest organisms classed as animals are generally larger than the vegetable cells just alluded to. They consist of protoplasm without any nucleus, and only sometimes with a structural difference between any part of their substance. As an example we may take *Protamœba*. This is a small mass of protoplasm without any nucleus, but its outer layer is clearer and less granular than the central part. It can move by sending out protoplasmic processes, in which currents can be observed resembling those in the vegetable cells. Except as regards the nucleus, it is much the same as the *Amœba*, which can be more readily watched, and will therefore be more accurately described.

The amœba is a single cell or mass of uncovered protoplasm, containing a well defined portion of substance or nucleus, within which is a small speck or nucleolus. The central part of the protoplasm is densely packed with coarse granules, but the outer more active part is structureless, and translucent-looking, somewhat like a fine border of muffed glass, encasing the coarsely granular middle portion. Such a one-celled animal has no special parts differentiated for special purposes, the requirements of its functions being so small that the protoplasm itself can accomplish them all.

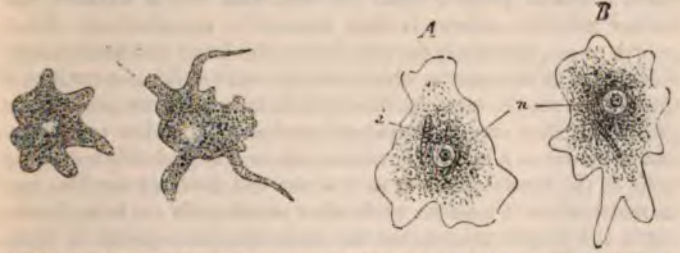


Fig 40.—Two different forms of Amœbæ in different phases of movement. Those on the left after Cadiat. A. and B. show an outer clear zone (Gegenbaur).

Thus the processes of protoplasm, which flow out with considerable rapidity from the body, commonly encircle particles of nutrient material, and then closing in around them, press them into the midst of the granular central mass. Here they sojourn some little time, and during this period no doubt any nutritive properties they possess are extracted from them, and they are then ejected from the plastic substance. This form of assimilation demands no previous preparation of the food such as we shall see takes place in the alimentary tract of man, and in the special organs of the higher animals; yet it is a form of digestion adequate at least to the requirements of this simple organism. The repeated alteration of the different parts of the protoplasm in relation to one another, and the surrounding medium during the flowing hither and thither of the currents, produces not only a change in the shape and position of the animal, but also acts as a means of distributing the nutriment to the different parts of the body, and of collecting and carrying to the surface the various products of tissue-decomposition; thus the streaming protoplasm does the work of a circulating fluid such as we see in the more elaborate organisms for the distribution of nutriment and elimination of waste materials. The surface of the amœba is sufficient to allow of the gas-interchange necessary for life, and by means of the ever-changing material exposed, sufficient oxygen is taken for its tissue combustions, and so a function of respiration is established. The growth that results from the perfect performance of these vegetative functions proceeds until the maximum size is attained, and further nutritive activity is then devoted to reproduction. When growth ceases, commonly the cell divides and forms two distinct individuals. The movements which form the most striking operations of the amœba are the same as those which take place in protoplasm, except that they are more rapid and obvious. The clear outer layer first flows out as a bud-like process, and, as it is gradually enlarging, some of the central granular part of the cell suddenly tumbles into its midst, where it remains, while other pseudopodia are being thrown out in the neighbourhood, and the same changes repeated in them. It is difficult to watch the motions of an amœba without being impressed with the idea that it is not only endowed with sensibility but that it also can discriminate between different objects, for we see it greedily flowing around some food material, whilst it carefully avoids other substances with which it comes in contact.

If a glass vessel, containing several amœbæ, be placed in a window, they will be found to cluster on the side of the glass most exposed to the light. From this it would appear that, in some obscure way, protoplasm can appreciate light, and respond to its influence by moving towards it.

This single-celled animal—or nucleated mass of protoplasm, can perform all the functions of a higher animal. It can move from place to place and assimilate nutriment, apparently discriminating between different materials. It distributes nutrient stuffs and oxygen throughout its body by a kind of tissue circulation, and it can appreciate and respond to the most delicate form of stimulus, namely light, which subtle motion has no effect on the sensory nerve-fibres of the higher animals.

In some unicellular animals certain parts of the cell are specially modified for the performance of special functions, a division of labour thus taking place which insures the more perfect accomplishment of the different kinds of activity. In one of the commonest of the Infusoria (*Paramœcia bursaria*), which swarm in dirty water, this is well exemplified. The outer layer of the flattened body is denser, and forms a kind of fibrillated cortical case (ectosarc), which is covered over with hair-like processes (vibratile cilia), which constantly move in a certain direction, so as to propel the creature rapidly through the water. The internal part of the cell is very soft, almost fluid, and coarsely granular in appearance, containing many bodies which have obviously been introduced from without. This soft internal protoplasm (endosarc) moves slowly round in a definite direction, completing its circuit in one or two minutes, and thus carries on a circulation which mixes the various matters contained in it. At one point of the ectosarc, or cortical layer, an orifice or mouth leading to an œsophageal depression is found. This orifice is lined by moving cilia, which by their vibrations drive the food into the œsophagus, whence it is periodically jerked into the soft internal protoplasm or endosarc, together with some water, and thus forms a food vacuole, which is carried round in the circulation of the ectosarc. Besides a well-marked nucleus and nucleolus in the central part of the cell, these paramœcia have one or more clear spaces placed near the surface at the extremities of the animal. These vacuoles suddenly contract, and disappear every now and then. When this contraction occurs fine canals radiating from the contractile vacuole are distended with the clear fluid which has probably entered the vacuole from without. Thus a permanent set of water vessels carry fluid from the contractile vacuole throughout the endosarc.

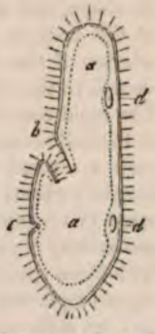


Fig. 41. — Diagram of Paramœcium showing digestive cavity. (*a a*) Body space filled with soft protoplasm, into which food is taken. (*b*) Mouth. (*c*) Anus. (*d*) Contractile vesicle. (After Lachmann.)

In such an animal there is a distinct advance of function compared with the amœba: a more elaborate and specialised method of feeding: a more systematic and regular circulation of nutrient matters: a respiratory distribution of water by the contractile vesicle and its water canals; more rapid motion; and more obvious sensation.

In the bell animalcule, or vorticella, the same kind of division of labour exists, but in one of its commonest conditions it is attached by a thin stalk to the stalk of some weed or other object. Besides the ciliary movement we here find that the general mass of the protoplasm can suddenly and forcibly contract, so as to completely alter its shape, and change the bell into a rounded mass. This spasm of the body is commonly associated with a wonderfully rapid contraction of the stalk. This stalk consists of a delicate transparent sheath, in the centre of which is a thin thread of pale protoplasm. The rapid contraction of the protoplasm of the stalk and the spasm of the bell occur on the application of the least mechanical excitation, such as a touch to the cover-glass. Here in a single cell we have certain portions set apart for special purposes, most of which are the same as in paramœcia. But the animal being attached requires a special way of escaping from its enemies, and hence we find it endowed with three special forms of motion. Besides the ciliary and streaming protoplasmic motion, its body can spasmodically change its shape, and the stalk contracts with a velocity comparable with that of the most specially modified contractile tissue (muscle) of the higher animals, by means of which their rapid and varied movements are carried out.

CHAPTER V.

NUTRITION AND FOOD-STUFFS.

THE continuation of protoplasmic life depends on certain chemical changes which are accompanied by a considerable loss of substance. This loss must be made good by the assimilation of material from without, and the manner by which it is obtained constitutes one great point of difference between Plants and Animals. In the majority of the former (certain fungi form the main exceptions) the cells in those portions of the plant which are exposed to the light and air, contain a peculiar green substance called chlorophyll, and through the agency of this substance they are able to obtain from the inorganic kingdom nearly all the food they require. Water is taken up by the roots with such salts as may happen to be in solution, and is carried through the stem to the leaves; here the active chlorophyll-bearing cells, under the influence of the sun's rays, cause it to unite with the carbon dioxide present in the air, to form various substances, of which we may take starch or cellulose as the simplest example. This reaction may be represented chemically, thus :—

$$6\,CO_2 + 5\,H_2O = \underbrace{C_6H_{10}O_5}_{\text{Starch or cellulose.}} + O_{12}$$

A large proportion of oxygen is thus set free and discharged into the atmosphere.

The most striking property of plant protoplasm is, then, the power of using the energy of the sun's rays to separate the elements of the very stable compounds, carbon dioxide and water, and from the elements thus obtained to make a series of more complex and unstable compounds, which readily unite with more oxygen, and change back to carbonic anhydride and water.

The new carbon compounds made in and by the protoplasm of the green plants are some of the so-called "organic compounds," which enter into the composition of both plants and animals, and form an essential part of the food of the latter. They may be divided into three groups—

i. Carbohydrates—bodies so called from the presence of hydrogen and oxygen in the proportion to form water; *e.g.*:—

Starch, $C_6H_{10}O_5 = C_6(H_2O)_5$
Grape sugar (dextrose) $C_6H_{12}O_6 = C_6(H_2O)_6$
Cane sugar (sucrose) $C_{12}H_{22}O_{11} = C_{12}(H_2O)_{11}$

ii. Hydrocarbons—compounds of carbon and hydrogen with a less proportion of oxygen than Division i., as oils and fats—

Olein (principal constituent of olive oil), $C_{57}H_{104}O_6$

iii. Albuminous bodies which contain nitrogen in addition to carbon, hydrogen, and oxygen. These are of very complex composition, and, as yet, cannot be represented by chemical formulæ.

Animals, on the other hand, cannot thrive on the simple forms of food obtainable from the inorganic kingdom, which suffice for the nutrition of a plant. They require the materials for their assimilation to be nearly allied in chemical composition to their own tissues. In short, they require as food the very organic substance which the plants spend their lives in making: viz., starches, fats, and albuminous bodies. These substances must, therefore, be supplied to animals ready made, as they are produced by plants. Directly or indirectly, through the medium of other animals, all these complex substances which form fuel so useful to our economy, are derived from the work done by vegetable life.

The chief acts of animal protoplasm are really oxidations, a slow burning away of its substance, which results in the production of inorganic materials like those used by plants as food.

Plants, then, use simple food-stuffs, and from them manufacture complex combustible materials, and thus store up the energy of the sun's rays in their textures.

Animals use complex food-stuffs to renew their tissues, which they are constantly oxidising, and by this means the energy for the performance of their various active functions is set free.

Although the various kinds of food-stuffs used by animals are so highly organised in comparison with those used by plants, yet they cannot be admitted at once into the economy without having undergone a special preparation, which takes place in the digestive tract where the various food-stuffs are so changed as to allow them to pass into the fluids of the body.

We shall first consider the chief varieties of food-stuffs, next their preparation for absorption, and then the means by which they are distributed to the tissues. The last step in tracing the assimilation of the food is to follow the intimate processes which go on between the blood carrying the nutriment, and the different tissues. This most interesting but difficult question shall receive our attention in a subsequent section.

Food.—There are two portals, namely, the lungs and the alimentary canal, by which new materials normally enter the animal body.

Within the lungs the blood comes into close relation with the air, and takes up oxygen from it. The oxygen is then carried to the various tissues, where it aids the combustion accompanying the life and functions of these tissues. Although oxygen is the most abundant element in the body, taking part in almost every chemical change, and its continuous supply is more immediately necessary for life than that of any other substance, yet it is not counted as food, because tissue oxidation is artificially distinguished from tissue nutrition.

The details of the union of oxygen with the blood will be found in the Chapter (XIX.) on Respiration.

It is then only to the liquid and solid portions of the material income of an animal—that, in short, which it must busy itself to obtain—that the term "food" is applied. These are introduced into the alimentary canal, where the truly nutrient materials are separated and prepared for absorption into the blood, while the portions which are not useful for nutrition are carried away as excrement. One is, therefore, quite prepared to hear that the really nutritious food-stuffs are composed of materials which are chemically like the tissues, although, as we shall see, we have no grounds for believing that the different chemical groups of nutritive stuffs are exclusively destined to replace corresponding substances in the body. On the contrary, we have good reason to think that within the body the conversion of one group into another is very common.

In Chapter III. the tissues of the animal body were shown to consist of chemical compounds, which have been classified into certain groups. And it has also been stated that the tissues are constantly undergoing chemical changes inseparable from their life, and that for these changes a supply of nutritive material is necessary.

The nutriment required for an animal is, then, made up of substances which may be divided into the same chemical groups as the tissues of the body: viz., proteids, fats, carbohydrates, salts, and water. So that each of the various substances which we make use of as food, contains in varying proportions several of the different kinds of nutrient material, either naturally or artificially mixed so as to form a complex mass, the important item water being the only one which is commonly used by itself. These substances may be considered to be the chemical bases of the food, as they are also the chemical bases of the animal body.

The following classification shows the relationships between the chief items of nutritious matters, from a chemical point of view, and their distribution in the various foods we commonly eat.

I. ORGANIC.
  1. Nitrogenous—
    A. Albuminous—abundant in eggs, milk, meat, peas, wheaten flour, &c.
    B. Albuminoid—in soups, jellies, &c.
  2. Non-Nitrogenous—
    A. Carbohydrates (sugar, starch)—abundant in all kinds of vegetable food, and in milk, and present in small quantity in meat, fish, &c.
    B. Fats—in milk, butter, cheese, fat tissues of meat, many vegetables, oils, &c.

II. INORGANIC.
  1. Salts—mixed with all kinds of food.
  2. Water—mixed with the foregoing or alone.

The nutritive value of any kind of food depends upon a variety of circumstances, which may be thus summed up :—

I. *Chemical composition*, of which the main points are—

(1.) The proportion of soluble and digestible matters (true food-stuffs) to those which are insoluble and indigestible (such as cellulose), &c.

(2.) The number of different kinds of nutrient stuffs present in it.

(3.) The relative proportion of each of these chemical groups.

II. *Mechanical Construction.*—The relation of the nutrient to the non-nutrient parts is of the greatest importance, as is seen where the nutritious starch of various vegetables is enclosed in insoluble cases of cellulose, which, if not burst by boiling, prevent the digestive fluids from reaching the starch.

III. *Digestibility.*—This depends partly upon how the substances affect the motions of the intestines, and partly upon their construction. Thus, some substances, such as cheese, though chemically showing evidence of great nutritive properties, by their impermeability resist the digestive juices, and are poor aliments.

IV. *Idiosyncrasy.*—In different animals and in different individuals, and even in the same individuals under different circumstances, food may have a different nutritive value.

Chemically, then, foods are composed of a limited number of elements similar to those found in the animal tissues, viz., carbon, oxygen, nitrogen, and hydrogen, together with some salts. If nothing more were needed by the economy than a supply of these elements and salts in a proportion like that in which they exist in the tissues, such could be easily obtained from inorganic sources; but, as has already been stated, it is necessary that an animal obtain these elements associated in the form of organic materials of complex construction (namely, proteids, &c.) ready made. Allowing the necessity of organic food, it might be supposed that since the elements exist in proper proportion in the proteids, an abundant supply of proteids would suffice for all nutritive purposes, and alone form an adequate diet. Theoretically, proteid alone ought to be sufficient for nutrition. It, however, has been frequently tested by experiment, and practically decided, that an animal will not thrive upon a free supply of pure proteid food alone; and in the human subject such exclusive diet would induce dangerous abnormal conditions in a short time. Since nitrogen is an important element in nearly all parts of the body, we could hardly expect that a diet composed of non-nitrogenous food-stuffs alone could support the animal economy. In short, the results of numerous experiments show that no group of the food-stuffs already enumerated can alone sustain the body, but rather that a certain proportion of each is absolutely necessary for life.

SPECIAL FORMS OF FOOD.

The articles of diet we make use of are *animal* or *vegetable*, according to the source from which they are derived. It will be seen that a varying quantity of all chemical classes of food-stuffs are generally present in most kinds of food, whether animal or vegetable. The following diagram shows the proportion of the more important food-stuffs in some examples of the materials commonly used as food :—

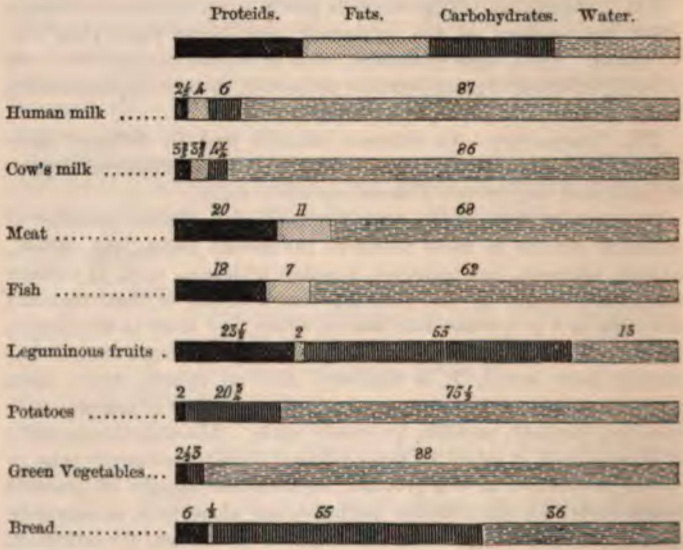


Fig. 42.—Diagram showing the per-centage of the principal food-stuffs in a few typical comestibles. The numbers indicate the per-centages. Indigestible materials are omitted.

Among animal foods are included milk, the flesh of various animals, and the eggs of birds. These may be more fully described as typical examples.

Milk.—For a certain period of their lifetime the secretion of the mammary gland forms the only food of all mammals, and it is the one natural product which when taken alone affords adequate nutriment. It consists of a slightly alkaline watery fluid, containing :—

1. Proteids, in solution.
2. Fats, finely divided to form perfect emulsion.
3. Sugar, in solution.
4. Salts, in solution.

Owing to the action of certain organisms which readily propagate in milk if exposed to the air at a warm temperature for some time, it loses its alkaline reaction, and becomes sour from the formation of lactic acid from the milk sugar, by a kind of fermentation, the probable equation for which may be written thus :—

$$\underset{\text{Milk Sugar.}}{C_6 H_{12} O_6} = \underset{\text{Lactic Acid.}}{2C_3 H_6 O_3}.$$

If fresh good milk be allowed to stand, the fatty particles tend to float to the surface, thus forming a layer of cream.

The milk of different animals is similar in all essential points, but differs slightly in the relative proportion of the ingredients, as may be seen in the following table :—

	Human.	Cow.	Goat.	Ass.
Water	889·08	857·05	863·58	910·24
Casein	39·24	48·28	33·60	20·18
Albumin ...		5·76	12·99	
Butter	26·66	43·05	43·57	12·56
Milk Sugar ...	43·64	40·37	40·04	57·02
Salts	1·38	5·48	6·22	
Solids	110·92	142·95	136·42	89·76
	1000.	1000.	1000.	1000.

Milk varies both in the amount of solids in solution, and fat, according to the age and general condition of the animal, period of lactation, time of day, &c.

Since human milk is much poorer in proteid, fat, and salts (see Table), and richer in sugar, than that of the cow and other domestic animals, it is necessary to dilute the latter with water, and add sugar, when it is substituted for human milk in feeding infants.

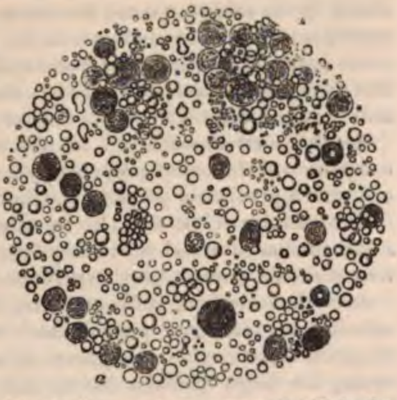


Fig. 43.—Microscopic appearance of milk in the early stage of lactation, showing colostrum cells (*a*).

The great value of milk as nutriment depends upon the fact that it contains every class of food-stuff, viz., proteids, fat, carbohydrates, salts, and water, in the proportion demanded by the economy; the salts in milk being those required for building up the bones of the infant, viz., phosphates and carbonates of lime, &c.

The normal variations in these proportions are not very great, but as artificial modifications of the per-centage of water are common, a knowledge of the method of testing the purity of milk is necessary.

Milk Tests.—The specific gravity of milk gives an easy measure of the solids in solution, but unfortunately it gives no estimate of the amount of fat suspended in the emulsion. Therefore, to test milk adequately two methods must be employed: one to estimate the degree of density of solution, and the other the degree of opacity of the emulsion.

I. To test the density, a specially graduated form of hydrometer is generally used. This is graduated so as to indicate specific gravities from 1042 to 1014. The former being the maximum density of pure milk, the average being about 1030, and the latter being about the density of pure milk when mixed with an equal bulk of water. Every reduction of 3 in the specific gravity may be said to correspond to about 10 per cent. of water.

II. The degree of opacity is estimated by the amount of water required to render a small quantity of milk sufficiently translucent to allow a candle-flame to be seen through a layer of the mixture one centimetre thick. One cubic centimetre of the milk (which has been shown by the microscope and the iodine test not to contain chalk or starch) is placed in a test-glass with flat parallel sides, just one centimetre apart, and water is cautiously added from a graduated pipette. The more water required the richer the milk is in fat; good fresh milk requires about 70 times its bulk of water to become translucent.

Another method employed for the same purpose consists in the comparison of the colour produced by a thin layer of milk in a black cell with a previously prepared standard of greyish colours.

The quantity of fat may also be estimated by placing the milk in a tall graduated vessel for twenty-four hours, at the end of which time it should show at least 10 per cent. of cream.

Butter is made from milk, or better from cream, by breaking by agitation the coating of proteid which before churning prevents the oil globules from running together. It is almost completely composed of fat, the larger globules having run together to form the solid butter, which can be removed, leaving some small fat globules with the proteids, milk sugar, lactic acid, and salts in the water forming "butter milk." *

---

* For the details of secretion of milk, &c., see Mammary Gland.

Cheese is another form of food made from milk by precipitating the proteid either by lactic fermentation, or the addition of rennet—an extract of calves' stomach which, without the presence of any acid, curdles milk—and draining off the solution of milk sugar, and salts ("whey"). It contains most of the proteid, and a great deal of the fat of the milk. During the ripening of the cheese more fat is formed, apparently from the proteid, while leucin and tyrosin also appear.

Meat.—We use the flesh of the vegetable-feeding mammals and birds that are most easily obtainable, and many kinds of fish. The invertebrate animals, mostly shell-fish, need hardly be mentioned in a physiological dietary, and are not spoken of as meat.

As it comes from the butcher, meat consists of many of the animal tissues, the chief ones being flesh (muscle tissue), fat, and some sinews (fibrous tissue). The fleshy or lean part of meat is chiefly made up of nitrogenous materials, and contains: (1) Several proteids, chiefly the globulin, *myosin;* (2) gelatine yielding substances; (3) carbohydrates, glycogen, and sugar; (4) small quantities of fat; (5) several inorganic salts; (6) extractives.

Meat may be eaten raw, but as it is impossible to impart to it the various flavours which our artificial tastes demand without some special preparation, it is generally cooked before use. Moreover, the not infrequent occurrence in muscle of parasites which would prove injurious if swallowed alive, makes the exposure of meat to a temperature high enough to ensure their destruction advisable.

Apart from pleasing the taste, it is of great importance so to prepare meat as to preserve in it all the nutrient parts, many of which are soluble in water, and therefore are apt to be removed if that solvent be injudiciously used. Thus, the process of roasting, in which all its nutrient parts are retained, ought to be more satisfactory than boiling, by which the salts, extractives, carbohydrates, gelatin, and some albumin may be dissolved by the water. However, if the meat be plunged into water which is already boiling, the proteids near the surface are rapidly coagulated, and the water cannot reach the central parts in sufficient quantity to remove even the soluble ingredients. The whole of the albuminous parts may be thus coagulated as the temperature of the inner parts rises to boiling point. In treating meat to obtain "stock" ("bouillon") for the foundation of soups, the opposite procedure is adopted. Cold water is used, and the temperature slowly and gradually raised, but not quite to boiling point, in order that as much as possible of the soluble materials may be exracted, and a tasteless friable muscle tissue remains, ("bouilli").

As the fluid is generally allowed to boil in order to clear it, much of the proteid material which was dissolved in the earlier stage, is coagulated and removed with the scum. Although "stock" cannot contain any great proportion of the most important constituents of meat, it is of much value as a nutriment in medical practice, possibly on account of some stimulating action of its ingredients upon the motions of the intestines and heart. A strongly albuminous extract of meat "beef-tea," may be made by digesting flesh in a small quantity of water, and keeping the temperature below that at which albumin coagulates, and adding vinegar and salt to facilitate the formation of syntonin and the solution of myosin. The salt can be then removed by dialysis.

Eggs. Eggs consist of two parts, one the white, composed of albumin, and the other, the yolk, chiefly made up of fat.

The white is a concentrated watery solution of albumin, held together by delicate structureless membranous meshworks. Besides the albumin it contains traces of fat, sugar, extractives, and salts.

The yellow fat emulsion of the yolk contains a peculiar proteid, vitellin, some grape sugar, and some inorganic salts, in which combinations of phosphoric acid and potassium are conspicuous. Raw eggs are difficult of digestion, as is all uncooked albumin. Hard boiled eggs, if not finely divided by mastication, are also very difficult to digest, for the gastric juice cannot penetrate the hard masses of coagulated albumin which are so easily and commonly swallowed. Eggs, when lightly cooked, are easily digested, as the albumin is already coagulated, and cannot be introduced into the stomach in large masses. Eggs are of very great nutritive value, as they contain so large a per-centage of proteid, fats, and salts.

Vegetable Food.—Vegetables differ from animal food :—

(1.) In containing a much greater proportion of material which for man is indigestible (cellulose), and a less proportion of real nutritive material.

(2.) The per-centage of proteid is below that of animal food, and the proportion of carbohydrates is generally much greater, while the amount of fat is small but varies considerably. In order therefore to get the required amount of nutritive material from a purely vegetable diet, it is necessary to consume a much greater quantity and the amount of excrement indicating the indigestible matters is proportionately increased.

Cereals.—The most valuable forms of vegetable food are those obtained from the seeds of certain kindred plants (*Graminaceæ*) Wheat, rye, maize, oats, rice, &c., which when ground are used either as "whole meal," or, the integument ("bran") being removed, as flour. They contain different kinds of proteid. (1.) A native albumin soluble in water and coagulable by heat, and in many respects like animal albumin; but as it cannot be obtained pure it is imperfectly known. (2.) Vegetable fibrin, an elastic body, which coagulates spontaneously and is difficult to separate. (3.) Vegetable glue or gliadin, which gives the peculiar adhesiveness to the *gluten*, as the proteid mixture obtainable from corn is commonly called. Cereals also contain traces of fat, and a very large proportion of starch and some salts.

The following table gives the per-centages of the chief different nutritive stuffs in some common cereals:—

	Wheat.	Barley.	Oats.	Maize.	Rice.
Water	13	14·48	10·88	12	9·20
Proteid	13·53	12·26	9·04	7·91	5·06
Fats	1·58	2·63	4·	4·83	·75
Carbohydrates	69·61	67·96	73·49	73·19	84·47
Salts	2·	2·65	2·59	1·28	·5

Green Vegetables.—These contain some starch, sugar, dextrin, salts, and minute quantities of proteid, and are of small nutritive value.

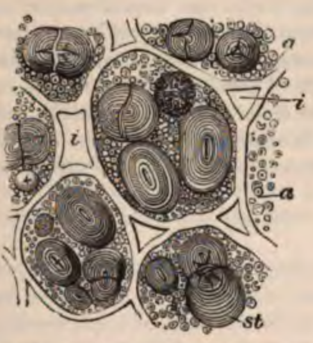


Fig. 44.—Section of Pea, showing starch and aleurone granules imbedded in the protoplasm of the cells. (After Sachs.)

a.—Aleurone granules. *st.*—Starch granules. *i.*—Intercellular spaces.

Potatoes contain very little proteid, but a considerable quantity of starch, upon which their nutritive value almost entirely depends.

The following table gives the relative proportions of the various *nutritive materials* contained in some of the common vegetable foods :—

	Peas.	Beans.	Potatoes.	Cauliflower.
Water................	14·50	12·85	72·74	79·18
Proteid	22·35	22·	1·32	·50
Carbohydrates...	56·61	56·65	23·77	18·
Extractive..... ...	1·18	3·32	·97	
Fats	1·96	1·59	·15	
Salts	2·37	2·53	1·05	·7

The most striking points are the very large proportion of proteid in the leguminous fruits, and the comparative richness of all vegetables in starchy food-stuffs.

Water is the great medium by the solvent power of which food is made capable of ingestion. Spring water always has a certain quantity of lime and other salts in solution, and in proportion to the amount of salts is said to be more or less hard. Water is tasteless, inodorous, and colourless when pure. Soft water, such as rain water, is pure, but not so agreeable to taste as spring water, and is very liable to contamination in its passage over roofs previous to collection. Standing water should be avoided for drinking, owing to the probability of its containing organic matter.

Salts.—Great varieties of salts are taken into the system, of which chloride of sodium forms the largest proportion. These have no doubt very important functions to perform, in entering into combination with the various tissues, and also probably in aiding the chemical changes of parts of which they do not form a normal constituent. They help to render certain substances soluble, and stimulate the cells of certain glands to more active secretion, *e.g.*, the kidney excretes more urea when there is an abundant supply of common salt in the food.

CHAPTER VI.

THE MECHANISM OF DIGESTION.

THE acts of digestion may be divided into *mechanical* and *chemical* processes. Under the *mechanical* processes come the arrangements for the subdivision, onward movement, and general mixture of the food. The chief objects of the *chemical* changes may be said to be the change from the insoluble to the soluble form of certain kinds of food-stuffs (starch, proteids) and the finer subdivision of others, such as fats, which do not dissolve in the intestinal or body juices.

Attention has already been called to the fact that there are different kinds of contracting textures, and that they are capable of different kinds of motion, some slow and steady, some rhythmical, some sharp, short and sudden. It must also be remembered that the more energetic and sudden the motions are, the more marked becomes the differentiation of the tissue. Thus the active, quick-contracting skeletal muscles and the rhythmically acting heart, are made up of tissue which is very distinct in structure and in mode of action from that of the contracting cells composed of ordinary protoplasm, while in the slowly moving internal organs we meet tissue elements which in different animals show many stages of gradation between simple, indifferentiated protoplasm and the special striated muscle tissue.

It is necessary that in the first stages of alimentation the motions should be quick and energetic; so the mouth, pharynx, and upper part of the œsophagus are supplied with striated muscle tissue, which differs in function and structure from that of the rest of the alimentary canal. In the stomach and intestines the slower and more gradual kinds of motion are required, and here we find a good example of non-striated muscle tissue.

Around the extremity of the rectum is a band of smooth muscle, which remains in a condition of persistent or *tonic* contraction.

For further details concerning the muscle tissue the student must turn to the Chapter (p. 366) on that subject. Here, however, it may not be out of place to describe briefly the special character of the muscles found in the wall of the digestive tube and their general arrangement.

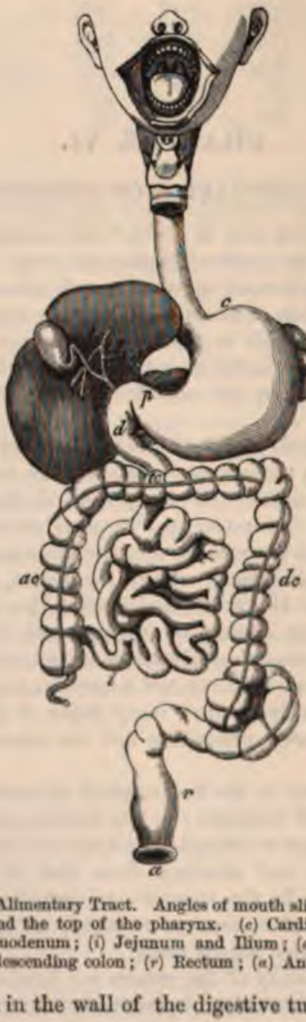


Fig. 45.—Diagram of Alimentary Tract. Angles of mouth slit to show the back of the buccal cavity and the top of the pharynx. (*c*) Cardiac; (*p*) Pyloric parts of stomach; (*d*) Duodenum; (*i*) Jejunum and Ilium; (*ac*) Ascending, (*tc*) transverse, and (*dc*) descending colon; (*r*) Rectum; (*a*) Anus.

Mastication.—In man, the introduction of food into the mouth is generally accomplished by artificial means, so that the biting teeth (incisors) and the tearing teeth (canines) are comparatively little used for obtaining a suitable morsel of food (Fig. 46). In the mouth the all-important act of chewing or mastication is accomplished by means of the motions of the lower jaw, the tongue, and the cheeks. This process of breaking up the solid parts of the food ought to be continued until all hard substances are ground into a soft pulp.

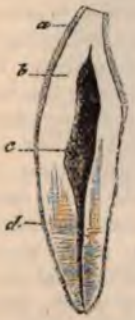


Fig. 46.—Transverse section of the Canine Tooth of a man. (*a*) Enamel; (*b*) Dentine; (*c*) Pulp cavity; (*d*) Crusta petrosa. (Cadiat.)

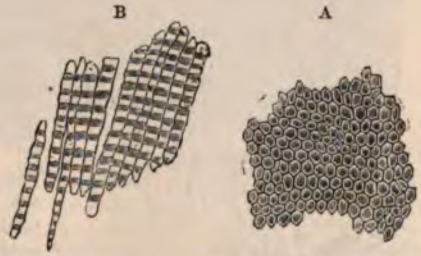


Fig. 47.—Structural elements of the Enamel of Tooth. A. Prisms cut across showing the hexagonal section. B. Isolated prisms. (Kölliker.)

Structure of the Teeth.—The exposed part of the teeth is covered by a dense substance of flinty hardness called *enamel*, which is developed from the epithelium, and consists of hexagonal prisms set on end, which are really modified epithelial cells but only contain about 2 per cent. of animal matter (Fig. 47). The bulk of the tooth is made up of *dentine*, a substance like bone in composition, pierced by numerous fine canals — dentine tubes — which radiate towards the surface, from the *pulp cavity*, in the centre of the tooth. Processes of protoplasm run in the dentine tubes from the tooth cells, which line the pulp cavity and preside over the nutrition of the tooth. The cavity contains vessels, nerves, &c., which enter at the root of the tooth which is enclosed in a kind of modified bone tissue called *crusta petrosa*.

The two rows of grinding teeth, molars and premolars, (one on each ide) of the lower jaw are made to rub against the corresponding teeth in the upper fixed jaw by the combined vertical and horizontal movements induced by the action of the powerful muscles of mastication the temporal muscles, together with the masseters and internal pterygoids, all tending by their contraction to elevate the lower jaw and bring the teeth forcibly together. This action is opposed by the digastric, the genio- and mylohyoid muscles, which by their combined force depress the jaw and separate the teeth. The horizontal movements are in the main accomplished by the external pterygoid muscles, which, acting together, pull the lower jaw forward so as to make the lower teeth protrude beyond the upper. In this action they are opposed by the digastric and hyoid muscles. One external pterygoid on either side acting alone, advances that side of the lower jaw only, and thereby causes the lower teeth to incline towards the opposite side in a lateral direction. The two muscles acting alternately cause a horizontal motion from side to side. Thus, while the lower teeth are pressed firmly against the upper ones they are at the same time made to glide over them, either from side to side or backwards and forwards. By these movements the bruised food is soon pushed from between the teeth, and passes towards either the tongue or cheek. The morsel is soon replaced between the teeth by the action of the tongue on the one hand and the buccinator muscle in the cheek on the other.

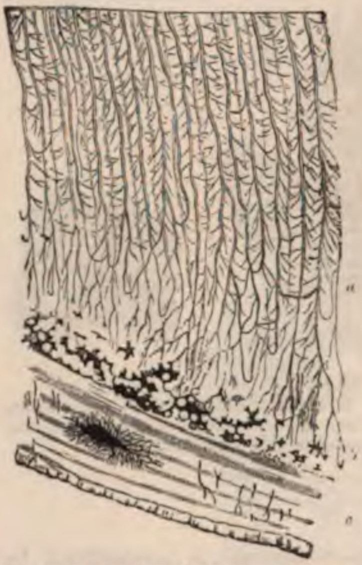


Fig. 48.—Section through a portion of the fang of a tooth. (*a*) Dentine tubules near the surface of the fang; (*b*) Granular layer; (*c*) Crusta petrosa.

While the process of mastication is going on, the food becomes thoroughly moistened with the fluid secreted within the mouth.

Deglutition.—The next step is swallowing. When the food is sufficiently triturated and moistened it is collected together by means of the tongue, and placed upon the upper surface of that organ, which becomes concave and presses or rolls the soft pulp against the hard palate so as to shape it into an oblong mass or bolus (Fig. 51). The apex of the tongue is now raised and pressed against the hard palate, and by the successive elevations of the different parts of the dorsum of the tongue the bolus is gradually pushed backwards towards the isthmus of the fauces. The root of the tongue with the hyoid bone is at the same

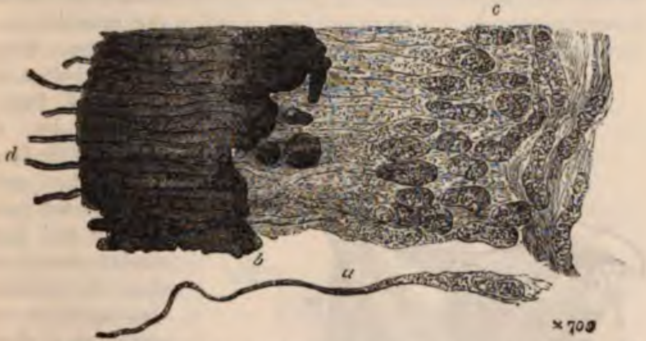


Fig. 49.—Section through a portion of dentine next the pulp cavity of a growing tooth. (*a*) An isolated odontoblast; (*b*) Growing part; (*c*) Odontoblasts. (*d*) Filaments of protoplasm projecting from the tubules of hard dentine. (Beale.)

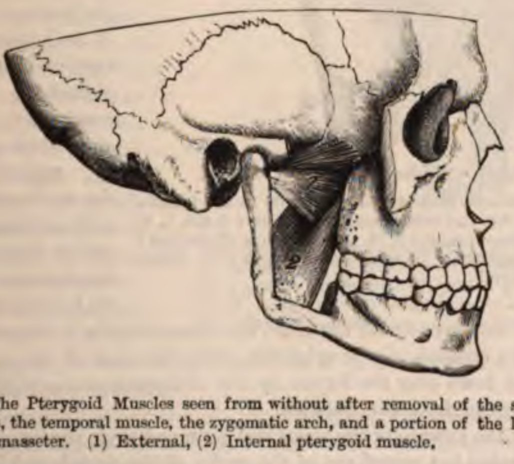


Fig. 50.—The Pterygoid Muscles seen from without after removal of the superficia parts, the temporal muscle, the zygomatic arch, and a portion of the lower jaw and masseter. (1) External, (2) Internal pterygoid muscle.

time drawn upwards and forwards, so that the bolus easily slips down along the retreating slope leading from the mouth cavity, and gets within the reach of the constrictors of the fauces. Immediately before the morsel of food is grasped by the muscles of the fauces the levator palati draws the soft palate upwards and backwards to completely close the posterior openings of the nasal cavity, as is shown by the fact that during the act of swallowing the pressure in the nasal cavity is raised. At the same moment the intrinsic muscles of the larynx, which surround the rima glottidis like a constrictor, firmly close that opening by approximating the cords and arytenoid cartilages. The entire larynx is at the same time drawn up behind the hyoid bone by the thyro-hyoid muscle. The rima glottidis is thus tucked in under the cushion of the epiglottis, while the leaf of the epiglottis is pulled down over the larynx by the oblique aryteno-epiglottidean and thyro-epiglottidean muscles.

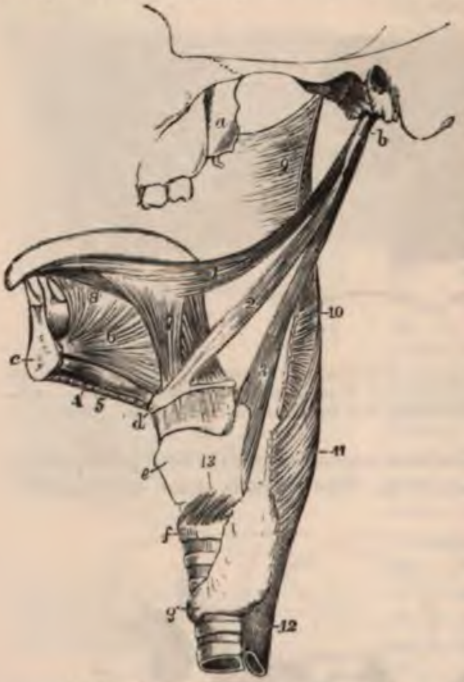


Fig. 51.—Muscles of Tongue and Pharynx.

1, 2, 3, Muscles from styloid process (*b*) to the tongue, hyoid bone (*d*) and pharynx respectively; 4, 5, 6, 7, 8, muscles of tongue; 9, 10, 11, constrictors of pharynx; 12, œsophagus; 13, is placed on larynx (*e*). (Allen Thomson.)

While the closure of the nasal and pulmonary air passages is going on, the bolus has passed out of the cavity of the mouth and has been caught by the palato-glossal and palato-pharyngeal muscles which force it into the pharynx, and at the same time close the isthmus faucium behind the descending morsel. The stylo-pharyngeis and the pharyngeal constrictors now grasp the bolus spasmodically, and the latter contract in rapid succession, moving the bolus onwards, and drawing themselves over it, pass it on to the œsophagus, where, by a progressing ring-like contraction of the circular muscles and a simultaneous shortening of the longitudinal layer of fibres the mass is slowly squeezed down to the cardiac orifice of the stomach. The movements of the œsophagus are essentially peristaltic in character, the peculiarities of which form of motion will be discussed when speaking of the intestinal movements.

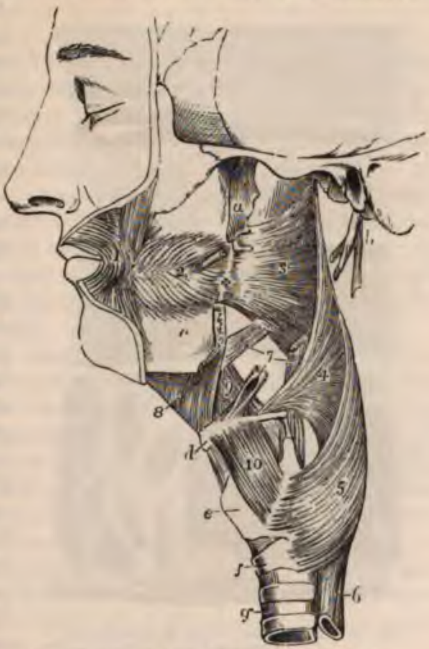


Fig. 52.—Deep Muscles of Cheek, Pharynx, &c.

(1) Orbicularis oris; (2) buccinator; (3) superior; (4) middle, and (5) inferior constrictors of the pharynx; (6) œsophagus; (7) styloid muscles cut across; (8, 9, 10) muscles attached to the hyoid bone (*d*) and thyroid cartilage (*e*). (Allen Thomson.)

The entire process of swallowing is a continuous series of co-ordinated muscular acts, quite independent of gravitation, as may be seen in animals drinking with their heads downwards. Although all the complex sets of movements follow each other perfectly evenly and without any check or pause, the act of deglutition is commonly divided into three so-called stages, between which, however, it is by no means easy to draw a hard and fast line.

The *first stage* is simply the initiatory step of placing the morsel of food or some liquid in such a position as to excite the second or spasmodic act of deglutition. This first step is a voluntary act, and it is the only part of the movements of swallowing over which we have any voluntary control. The progress of the morsel between the tongue and palate towards the fauces may be as slow and gradual as we wish, but the moment a certain point is reached volition is at an end, and we are unable to check the completion of the act.

By the *second stage* is meant the period occupied by the passage of the food bolus through the pharynx and past the top of the larynx. Although we are not able to influence it in any way by our will, we are conscious of the food passing in this region. It is a rapid involuntary spasm in which a great number of muscles take part, all of which are made up of striated muscle tissue.

The *third stage* includes all the rest of the time during which the bolus is passing from the grasp of the lower pharyngeal constrictor and along the œsophagus. Not only has our will no influence over this stage of deglutition, but we are hardly conscious of its taking place, since no sensations accompany the greater part of it. Thus the more essential movements of the act of swallowing are purely reflex and involuntary, though we can call forth this series of reflexions by voluntary stimulation of a certain part of the fauces by means of a morsel of food or a drop of liquid. And without such a stimulus as food or liquid we cannot by our will excite swallowing. We think we can perform the muscular movements of swallowing when we please, without any food or fluid, but in this we are mistaken, as careful observation of our own performance of the act will show.

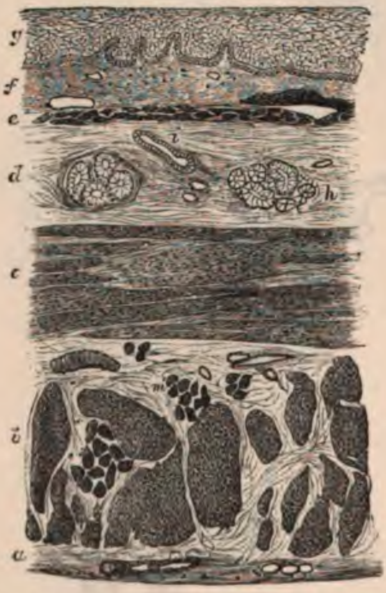


Fig. 53.—Transverse section of Œsophagus. (Horsley.)

a. Outer fibrous covering.
b. Bundles of longitudinal muscle cut across.
c. Transverse muscular coat cut obliquely.
d. Sub-mucous coat with glands in section.
e. Muscularis mucosæ.
f. Mucous membrane with cut vessels.
g. Stratified epithelium.

The pharyngeal spasm is always preceded by the deposition in the region of the isthmus faucium of some drop of saliva collected from the mouth or fauces themselves. In fact, without a slight preliminary movement of the posterior part of the tongue—which might be called the last act of mastication—the more essential stages of deglutition cannot be excited.

Nervous Mechanism.—The voluntary influences which regulate the motions of the muscles of mastication pass along the efferent branches of the fifth nerves (trigemini) which accompany its inferior division. The muscles which depress the jaw to open the teeth and the intrinsic muscles of the tongue are supplied by the ninth pair of nerves (except the posterior belly of the digastric, which has a branch from the facial, and the mylohyoid and anterior belly of the digastric, which are supplied from the third division of the fifth). The co-ordination of the movements of mastication and suction seem to reside in the medulla oblongata, but are obviously under the control of the will.

The afferent impulses which excite the nerve centres in the medulla, and give rise to reflex acts which cause the swallowing movements, pass from the mucous membrane of the fauces along (1) the descending palatine branches of the spheno-palatine ganglion and the second division of the trigeminus, also along (2) the pharyngeal branches of the superior laryngeal branch of the vagus to the medulla, where the co-ordination of pharyngeal spasm and œsophageal peristalsis is accomplished. Thence the efferent impulses pass along (1) the hypoglossal to the hyoid and glossal muscles, (2) the glosso-pharyngeal and vagus to the pharyngeal plexus to supply the constrictors, and (3) along the facial and fifth to supply the fauces and palate, as indicated by their anatomical distribution.

The act of deglutition can be readily excited in an animal which is deprived of all the nerve centres down to the medulla oblongata, and may also be seen in those human monstrosities (anencephalous foetus) which are born without the upper part of the brain being developed, but can both suck and swallow.

The movements of the œsophagus are reflections from the central nervous system (medulla), both sets of impulses (possibly the afferent and certainly the efferent) passing along the branches of the vagus.

It would appear that the normal peristaltic movements of the œsophagus are always initiated by a pharyngeal spasm, and that they form an inseparable sequel to it. Thus the wave of contraction passes along the entire length of the œsophagus, even when the bolus is stopped mechanically, and on the other hand a body introduced into the œsophagus without passing through the pharynx excites no peristaltic wave and remains motionless.

But it has been observed, in apparent contradiction to the foregoing statement, that the œsophagus when removed from the body, and therefore quite independent of the pharynx and its nervous connections, can be excited to move peristaltically. In this case the medulla or vagus can have no part in bringing about this wave of movement. To explain this discrepancy it may be urged that the local nerve and muscle mechanism in the tissues of the œsophagus are capable by themselves of carrying out peristaltic contraction independently of the central nerve organs, but that this power is, under ordinary circumstances, held in check by the vagus. The inhibition is temporarily suspended as a sequence of pharyngeal spasm, and consequently a wave of peristaltic contraction is excited in the œsophageal muscles, either in response to the direct stimulus of a passing bolus, or as a result of impulses reflected along the vagus channels from the medulla.

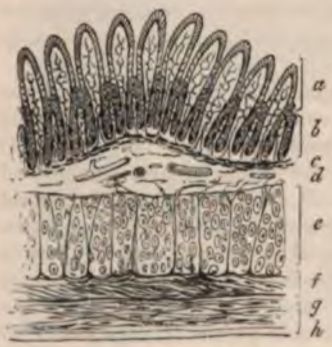


Fig. 54.—Diagram of Wall of the Stomach, showing the relative thickness of the mucous membrane (*a*, *b*, *c*), and the transverse (*e*), oblique (*f*), and longitudinal muscle fibres.

Motion of the Stomach.—The stomach and greater part of the intestinal tract move freely within the abdomen, being covered by the smooth serous lining of that cavity, which also keeps in position, so as to restrict their movements, those parts, such as the duodenum, into which the ducts of large glands open. When the stomach is empty it hangs with the great curvature downwards, and the muscular coats are quiescent. On being filled it is passively rotated on its long axis, so that the greater curvature is turned forwards, here meeting with less resistance, and the lesser curvature is turned backwards to its line of attachment. In the main, the motions of the stomach are peristaltic. They become very active about fifteen minutes after the introduction of food, and gradually become more and more energetic until the end of stomach digestion, which lasts about five hours.

The result of the peristaltic motion is to move the food, particularly the part next the gastric wall, along the great curvature towards the pylorus. A back current towards the cardiac extremity has been noticed running along the lesser curvature, and the median axis of the food mass. At the same time a peculiar rotatory motion of the gastric wall takes place, similar to that of rolling a ball between the palms of the hands, so that the food is twisted in a given direction, and the deeper lying portion is brought into contact with the mucous membrane.

While the fundus keeps up considerable pressure on the contents of the stomach, the indistinct peristaltic action of the central parts is intensified on nearing the pylorus into a strong circular contraction, which proceeds as a definite wave towards the pyloric valve, through which it gradually forces the more or less digested food. At first only the fluid parts are allowed to pass, but towards the later stages of digestion the fatigued pyloric muscle admits solid masses into the duodenum.

NERVE INFLUENCE ON STOMACH MOTIONS.—The stomach has nerve connections with the cerebro-spinal axis through the vagi, and the splanchnic branches of the sympathetic, and in the walls of the organ itself are numerous ganglion cells. The sympathetic connections do not seem to have any influence on the muscular coats, for neither their stimulation nor section has any marked effect on their movements. If the vagi be severed, stomach contractions still occur, but no form of local stimulation produces the normal gastric motions, even if the organ be quite full of food, therefore it would appear that the local nerve centres are not sufficient to excite the normal rhythmical muscular action. Moreover, stimulation of the cut vagi leading to the stomach causes active movements when the stomach is full. It is not merely the presence of food that produces the movements, as is shown by the fact that the motions increase as the contents of the stomach diminish, but conditions incidental to digestion (hyperæmia, &c.) probably also act as a stimulus.

VOMITING is the ejection of the contents of the stomach by means of a convulsive action of the respiratory and abdominal muscles associated with an abnormal contraction of the stomach wall, which aids in opening the cardiac orifice while it keeps the pylorus firmly closed.

The act of vomiting is commonly preceded by (1) a feeling of sickness or nausea, (2) a great secretion of saliva, (3) retching. The latter consists in a violent inspiratory effort in the midst of which the root of the tongue and larynx are raised and the rima glottidis suddenly closed so as to prevent air entering the wind-pipe. The inspiratory muscles still acting, and the pharynx and upper part of the œsophagus being held open, air is drawn into the gullet and dilates this tube nearly as far as the opening into the stomach. A contraction of the muscle fibres radiating from the œsophagus over the stomach, then opens the cardiac orifice and allows some gas to escape. Now the act of vomiting is completed if at this moment—the mouth and pharynx being open, the larynx closed, the œsophagus on the stretch, the cardiac orifice relaxed, and the pylorus firmly closed—the expiratory muscles forcibly contract, and, pressing upon the abdominal cavity, give a sudden stroke to its contents so as to empty the stomach. The wall of the stomach also contracts evenly throughout, but not with any forcible anti-peristaltic action such as would greatly aid in the operation of rapidly ejecting the vomit. The chief object attained in the adult by the action of the muscular coat of the stomach seems to be the relaxation of the cardiac orifice. In children, when the fundus is little developed, and the fibres radiating over the stomach from the œsophagus are numerous and strong, the act of vomiting requires less effort on the part of the respiratory muscles, the frequent puking of suckling infants being accomplished by the gastric muscle alone. When the vomit is emitted, the hyoidean, laryngeal, and neck muscles relax, and the air is forcibly driven out of the partially distended lungs so as to clear away any remaining particles from the upper part of the air passages.

Vomiting is usually caused by irritation of the stomach itself, and may be induced by either mechanical, electrical, or chemical stimulation of the mucous membrane. In this way some emetics, such as mustard, sulphate of copper, &c., act. It may also be caused by intestinal irritation, as when a hernia is strangulated, or the mucous membrane irritated by intestinal worms.

Gentle stimulation of the fauces and neighbourhood of the root of the tongue commonly induces vomiting. In the early stages of pregnancy the unusual condition of the uterus causes frequent vomiting, which is known as "morning sickness." The irritation of a calculus passing through the ureter, or a gall-stone impacted in the bile duct, commonly excite vomiting. Injuries of the brain, and psychical impressions, particularly those excited by the sense of smell or unusual disturbance of equilibrium, may give rise to vomiting. Moreover, a number of medicaments, as apomorphin, emetin, &c., cause vomiting if introduced into the blood.

From the foregoing facts it appears that vomiting is a complex and irregular muscular act, which may be induced by the stimulation of various parts of the internal surfaces of the body, particularly those which receive branches from the vagus nerve.

One would therefore be inclined to suppose that some afferent nerve channels exist in the vagus which bear impulses to a vomiting nerve centre and excite it, so as to cause it to send forth peculiar and irregular impulses to the respiratory, gastric, and other muscles, and give rise to their characteristic spasm.

In short, it would seem to be a reflex act, the afferent impulses of which pass to the medulla oblongata by the vagus, and the efferent impulses are conveyed by the ordinary spinal nerves to the respiratory muscles, by the vagus to the pharyngeal, laryngeal and gastric muscles, and by the fifth, seventh, and ninth nerves to the palatine, facial, and hyoidean muscles. This vomiting nerve centre must lie in the medulla, in very close relationship to the respiratory centre, with which it nearly corresponds. This centre may bring about the whole sequence of events known as vomiting when stimulated either directly by poisons, contained in the blood, indirectly through the vagus, or even from the higher centres by emotions or ideas. Section of the vagi renders vomiting impossible, as it cuts off both the commonest source of stimulus going to the centre, and also the important efferent impulses which cause the muscle coat of the stomach to contract and to open the cardiac orifice.

MOVEMENTS OF THE INTESTINES.—The muscular coats are somewhat differently arranged in the small and the large intestines, but have the same general relation to each other, viz., a thin longitudinal layer lying externally, next the serous membrane, and a layer of circular fibres considerably thicker lying internally under the mucous membrane. In the large intestine the external longitudinal fibres are collected into three bands placed at equal distances one from another, which, being rather shorter than the remainder of the intestine, throw the intermediate part into a series of pouches.

It is in the small intestine that peristaltic motion of the most typical kind occurs. A wave of contraction passes from the pylorus along the circular fibres, so as to look like a broad ring of constriction progressing slowly downwards.

The longitudinal fibres at the same time contract so as to shorten the piece of intestine immediately below the ring of constriction, and also cause a certain amount of rolling movement of those loops of intestine which are free enough to move.

This motion takes place periodically in proportion to the amount and character of the contents of the intestine, the food passing over the mucous membrane being to all appearance the stimulus which normally calls forth and intensifies the action.

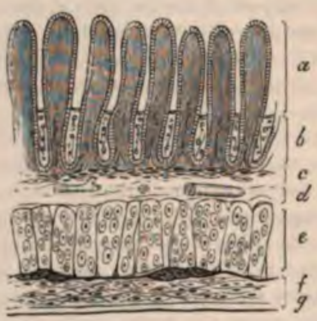


Fig. 55.—Diagram of a longitudinal section of the wall of the small intestine.

a. Villi.
b. Lieberkühn's Glands.
c. Muscularis mucosæ, below which lies Auerbach's nerve plexus.
d. Connective tissue in which many blood and lymph-vessels lie.
e. Circular muscle fibres cut across with Meissner's nerve plexus below it.
f. Longitudinal muscle fibres.
g. Serous coat.

The activity of the peristaltic movements varies with many circumstances besides the contents of the intestines. Of these the most noticeable is the amount and character of the blood flowing through the vessels of the intestinal wall. Thus stoppage of the blood current by tying the arteries or deficiency of oxygen and excess of carbonic acid causes inordinate activity of the peristaltic action. Direct irritation of the serous surface of the intestine, with mechanical, chemical, or electrical stimuli causes also increase in the movements of the intestine.

The great activity of the motion observed when the abdominal cavity of a recently killed animal is opened depends partly on the exposure to cool air, and partly on the venous character of the blood in the vessels no longer oxidised by respiration.

The irregular and impetuous action of the intestine which follows the constriction or strangulation of a hernial protrusion, chiefly depends on the mechanical effect, but also is probably intimately related to the interference with the blood supply consequent on the pressure exerted by the constricting band. Prolonged over-work often induces immobility of the intestinal wall, and hence we find the purging and vomiting, which accompany a temporary hernial constriction, followed by inability of the intestine to propel its contents.

These points have also been proved by results of experiments on the lower animals.

The movement of the large intestines are the same as the small, but not so obvious, owing to the modified sacculated shape of this part of the alimentary canal. The contractions of the colon begin at the ileo-cæcal valve where the peristaltic wave of the ileum ceases. The normal intestinal motions thus pass in an almost uninterrupted wave from the pylorus to the end of the gut, but when special sources of irritation exist, a wave may originate in almost any intermediate part of the intestine. A reversed "anti-peristaltic motion," as it is called, only occurs as a result of some intense local stimulation, such as the strangulation of a hernia, &c.

The motion produced by the substances contained in the intestine depends on their character. The solid parts excite more rapid movements, and the more fluid portions but slightly influence the intestinal peristalsis.

Thus the solids which make their way through the pylorus are seldom to be found in the jejunum, no matter at what period after a meal the animal be killed, whereas the folds of the mucous membrane are always bathed in a fluid creamy material during the entire period of digestion, and even for a considerable time after all the food has left the stomach.

Mechanism of Defæcation.—This is a point of much importance, for the evacuation of the lower bowel is intimately connected with feelings of comfort and health, and the insuring of its accomplishment, in illness, forms an essential part of the physician's duty.

The movements of the intestine cause the various excretions and indigestible parts of the food to pass towards the sigmoid flexure of the colon, where their onward motion is checked for a time by the strong circular muscle of the rectum (called the superior sphincter, or tertius by Hyrtl), which does not carry on the peristaltic wave. The materials here get packed into a more or less solid mass, which is gradually augmented after each meal.

The lower outlet of the alimentary canal is closed by two distinct sphincter muscles. One thin external superficial muscle, made up of striated fibres, belongs to the perineal group, and has little influence on the closure of the anus. The deep or internal sphincter, which is much stronger, surrounds the gut for rather more than an inch (3 centimetres, Henle) in height, and is one quarter inch thick. It is made of smooth muscle, and therefore capable of prolonged (tonic) contraction. It would appear, however, that this strong sphincter is a supernumerary guard to the anal orifice, which is but rarely called into action, for during the interval of rest between the acts of defæcation, the fæces do not come in contact with the portion of intestine surrounded by this muscle. The rectum for quite one inch above the sphincter is perfectly empty, being kept free from fæculent particles partly by a fold of the intestinal wall, and partly by the repeated action of the voluntary muscles in the neighbourhood, which by intensifying the angle that exists at this point, and flattening this inch of rectum, can squeeze back the approaching matters. Anyone familiar with the digital examination of the unevacuated rectum, knows that no fæces are met with for about two inches.

Considerable accumulation may take place in the sigmoid flexure without much discomfort ensuing, but when the rectum is distended, an urgent sensation of wanting to empty it is experienced, and the voluntary movements mentioned above, are performed by the levator ani and the neighbouring perineal muscles, with the object of preventing any substance reaching the part of the rectum immediately above the sphincter.

If the rectum be distended with fluid, the occasional anal elevation does not suffice to keep it back, and a continuous and combined action of the sphincters and levator ani, &c., is necessary to ward off the expulsion of the contents.

When the lower bowel is habitually emptied at the same hour daily—a habit which should be carefully exercised—the sensations of requirement to go to stool occur with great punctuality, or can be readily induced by the will, so that normal defæcation is reputed to be, and practically is, a voluntary act. But not completely so, for somewhat like swallowing, the later stages of defæcation, consist essentially of a series of involuntary reflex events which we can initiate by the will, but when it is once started, are powerless to modify until the reflex sequence is completed.

Under ordinary circumstances, the evacuation of the fæces is commenced by the voluntary pressure exercised on the abdominal contents by the respiratory muscles. The diaphragm is depressed, the outlet of the air passages firmly closed, and the expiratory muscles thrown into action, while at the same moment the muscles which close the pelvic outlet relax, and allow the anus to descend, so that the inferior angle of the rectum is straightened, and a voluntary inhibition of the sphincter is brought about. This voluntary expiratory effort seldom requires to be continued for more than three or four seconds before some fæcal matter reaches the part of the rectum just above the sphincter. When this has occurred, no further abdominal pressure is necessary (except when the masses of fæces are large and hard), for the local stimulus starts a series of reflex acts which carry on the operation. These consist of an increased peristaltic contraction of the colon and sigmoid flexure, the waves of which pass along the rectum. These waves are accompanied by synchronous rhythmical relaxation of the sphincter, which replaces its normal condition of tonic contraction.

The effect of the voluntary effort, and the amount of the abdominal pressure required, depend upon the consistence of the fæces. When quite fluid, they constantly tend to come in contact with the sensitive point of the rectum, and a voluntary effort is required to prevent the reflex series of events from taking place, a momentary relaxation of the sphincter with voluntary abdominal pressure is sufficient to eject the contents of the bowel. On the other hand, when the fæces are firm, time is required in order that the slowly acting smooth muscle may pass the mass onward. In common constipation, the difficulty is to get the solid mass down to the sensitive exciting point, in which case a few drachms of warm fluid, used as an enema, may awaken the necessary reflex movements.

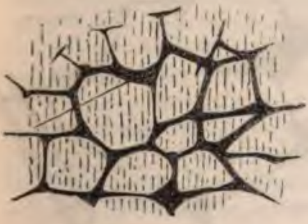


Fig. 56.—Auerbach's plexus from between the muscle coats of the intestine with low power.

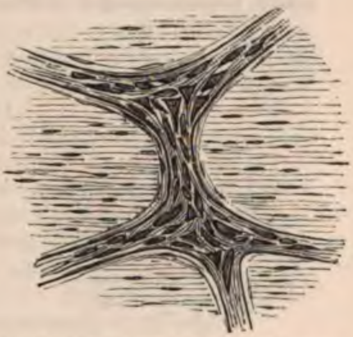


Fig. 57.—A nodal point of Auerbach's plexus under high power, showing the nerve cells.

Nervous Mechanism of the Intestinal Motion.—Many points in the nervous control exerted over the intestinal muscles are obscure. We know that intestinal movements which are peristaltic in their nature occur in a portion of intestine removed from the body, and thus separated from all central nervous control. We know also that there are abundant nerve elements in the walls of the intestines which have all the characters of ganglion cells, and therefore probably act as nerve centres. (Figs. 56, 57.)

With regard to these local nervous agencies, anatomists have made out two distinct sets, both of which have the form of a network of nerve fibrils studded with cell elements at their nodal points. One of these, a closely meshed plexus with flattened cords and ganglionic masses at their points of union, lies between the longitudinal and circular layers of muscle (Figs. 56, 57) forming the *plexus myentericus exterior* of Auerbach, and most likely has to do with the movements of these layers of muscle. The other lies internal to the circular muscle, in close relation to the muscularis mucosæ, and is called the *plexus myentericus interior* of Meissner; the meshes of which are looser and more irregular, and the cords and ganglia more rounded and finer than those of Auerbach's plexus. (Figs. 58, 59.)

The blood flowing through these nerve centres in all probability acts as a sufficient stimulus under ordinary circumstances, to produce some peristaltic motions, and hence we may say that they are automatic. When food comes into the intestine it increases the flow of blood, as well as mechanically irritating the intestinal wall. The intestinal vessels remain engorged so long as the process of digestion goes on.

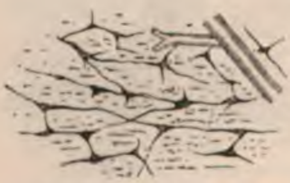


Fig. 58.—Meissner's plexus, low power.

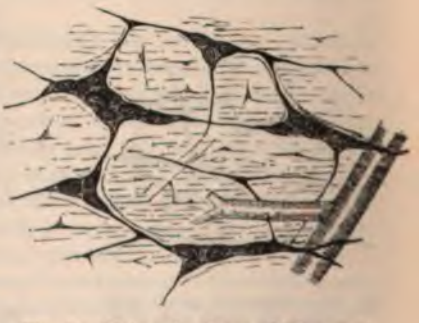


Fig. 59.—Meissner's plexus (high power), showing cells grouped at nodal points.

Food seems to act more effectually than insoluble mechanical stimuli, for when insoluble substances are placed in the gut, they at first call forth active movements; but these do not last long, for the stimulus is not of itself adequate to excite prolonged action, except it be associated with continuing congestion dependent upon other causes, such as the vaso-motor changes accompanying the general digestive process, and the absorption of the prepared food-stuffs.

With regard to the influence of other nerves, it seems to be admitted on all sides that the vagus acts as an exciting nerve, since stimulation of its peripheral part causes increased action, and it is probable that its great efferent channel for impulses is reflected through the brain.

On the other hand, the splanchnic nerves, which come from the thoracic sympathetic, are said to be inhibitors of the myenteric plexuses. This may be explained by their effect on the small vessels —which they no doubt control—causing a change in the blood supply. Be this as it may, the splanchnic seem to have considerable influence on the intestinal movements. When stimulated they commonly check the intestinal motions, but may sometimes (as when the movements have ceased after death), give rise to new movements.

On account of this double action, it has been said that there are two kinds of fibres, (1) inhibiting, which are easily excited, and during life have greater influence, and (2), exciting, which, though less excitable, retain their irritability longer.

However, most of these effects may be explained by referring them to vaso-motor changes.

With regard to defæcation, we know that a nerve centre exists in the lumbar portion of the spinal cord, which governs the sphincter, and seems to keep up its tonic contraction. This centre may be either excited to increased action or inhibited, by peripheral stimuli or by central influences from the brain.

Thus the local application of warmth causes inhibition of the centre, and thereby relaxation of the sphincter, while cold gives rise to increased central action, causing contraction of the sphincter muscle; (a point to be remembered when examining or operating within its grasp). Besides the voluntary variations which we can bring about in the activity of this lumbar centre, many other central influences, such as emotions, may operate upon it. Thus terror inhibits the centre, and loosens the sphincter independently of our will.

CHAPTER VII.

MOUTH DIGESTION.

THE cavity of the mouth is lined by a bright red mucous membrane, which is continuous with the skin at the lips. It varies in structure in different parts of the buccal cavity, and in its general construction more resembles the outer covering of the body than the mucous membrane lining the alimentary tract. It consists of (1) a superficial part composed of thick stratified epithelium, in the upper cells of which are flat, scaly, and tough, and are placed horizontally, while in the deeper ones the cells are soft, rounded or elongated, having their long axis perpendicular to the surface, and (2) a deeper part composed of fibro-elastic tissue, which, over the alveoli of the teeth, is amalgamated with the periosteum and forms the dense tough gums.

The mucous membrane of the mouth, is covered with papillæ, which on the dorsum of the tongue attain great magnitude and variety of shape and epithelial covering. In man, three kinds are described: — (1.) Narrow pointed, *filiform*. (2.) Blunt and clubbed at the apex, *fungiform*. (3.) Broad complex papillæ, surrounded by a fossa, *circumvallate*, of which there are but a limited number (about a dozen).

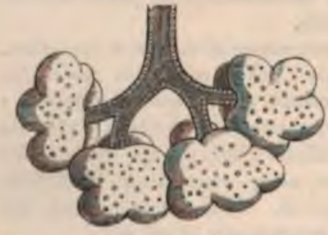


Fig. 60.—Diagram taken from a small portion of sacculated gland from Cockroach, showing branching duct and saccules.

The special secreting organs or glands, which pour their juices into the mouth, have all the same general type of structure, though they vary much in the detail as to the variety and character of their cells. They are known as the *acinous* or *sacculated* glands, from their being made up of numerous *acini*, or minute elongated sacs or tubules, arranged at the end of a repeatedly branching duct, like grapes on the terminals of the successive little branches growing from the central stalk to form a bunch. In the glands the saccules are packed together closely around the ducts, and by mutual pressure are made to assume various shapes. The wall of the saccule is formed of a very delicate clear transparent membrane, on the outside of which are numerous flattened branching stellate cells, the branches of which anastomose one with another, and appear also to penetrate the membrane in order to reach the inside of the acini.

The cavity of the little sacs is almost completely filled with large polygonal *gland-cells*, so that only a very narrow space exists in the centre. (Fig. 61.) From this space, there is free communication to the main duct of the gland by means of the proper ductlet of each saccule.

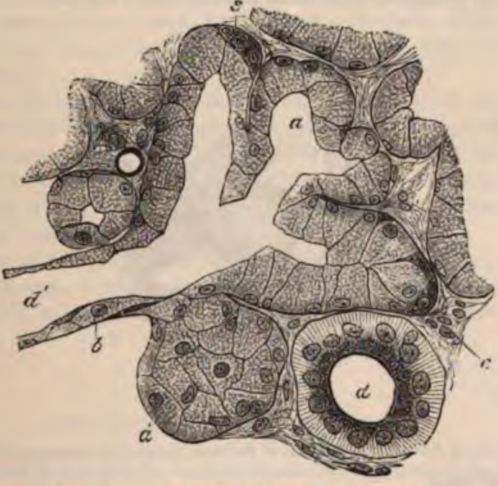


Fig. 61.—Section of the Sub-maxillary Gland of the Dog, showing the commencement of a duct in the alveoli. × 425. (Schäfer.)

a. One of the alveoli, several being grouped round the ductlet (*d'*).
b. Basement membrane in section.
d. Larger duct with columnar epithelium.
s. Half-moon group of cells.

In the saccules of some glands, the so-called mucous salivary glands, another kind of cell element is seen between the gland cells just described and the wall of the sac, their outer side following accurately the concave boundary of the saccule, their inner side impinging upon the gland cells. They thus acquire a more or less half-moon shape. These demilune cells will be again referred to (page 106).

Between the saccules are numerous blood vessels which branch and form a network of capillaries on the outside of each little sac.

Numerous nerves are also found, which, according to some observers, have ganglionic cell-connections in the gland substance, and send terminals into the gland-cells direct.

Although this account of the nerve terminations in the secreting cells of other glands has met with doubt, it is certain that in the lower animals nerve terminals have been traced into gland-cells, and upon physiological grounds, as will presently appear, we are forced to believe that a similar connection must exist in mammalia.

The ducts are lined with ordinary cylindrical epithelium which does not appear to have any secreting function. All the glands are made up of numerous packets of lobules bound together in one mass.

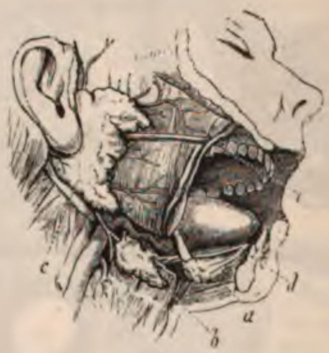


Fig. 62.—A dissection of the side of the face, showing the Salivary Glands.

a. Sublingual gland.
b. Submaxillary glands with their ducts opening on the floor of the mouth beneath the tongue at (*d*).
c. Parotid gland and its duct, which opens on the inner side of the cheek.

Each of these lobules is itself a perfect gland, so that even the smaller mouth-glands are separable into lobules, and hence are called compound acinous glands.

The mouth-glands are divided into two sets, which produce different kinds of secretion :—(1.) *Mucous glands*, which secrete *mucus*, and (2.) *Salivary glands*, which produce watery *saliva*. The functional distinction is seldom absolute, for most salivary glands have a mixed secretion, and various gradations of the transition from purely salivary to purely mucous glands can be made out.

The proper *mucous glands* are small, varying in size from a pin's head to a pea. They are found in groups under the mucous membrane in various parts of the mouth, and from their positions are called labial, buccal, &c. Their cells contain a clear muciginous substance.

The great *Salivary glands* are the three large glands which are known as the parotid, submaxillary and sublingual. On account of their great size they form striking anatomical objects, being large masses of irregularly arranged glandular packets, which might be spoken of as lobes to distinguish them from the smaller packets or lobules. Their ducts are of considerable size, and have strong walls made of dense fibrous tissue, containing many elastic fibres, and in one of them, the submaxillary, smooth muscle tissue has been demonstrated.

The parotid duct (Steno's) opens into the mouth about the middle of the cheek just opposite the second molar tooth. The submaxillary has also a single duct (Wharton's) which opens beneath the tongue beside the frænum. The sublingual gland has several ducts, some of which open into that of the submaxillary, and others unite to enter the mouth beside Wharton's duct.

In different animals and in different glands of the same animal a variable amount of mucus is secreted by these glands, which, however, are all called salivary, though the parotid alone deserves the name.

THE CHARACTERS OF MIXED SALIVA.

The liquid in the mouth is a mixture of the secretion of the salivary glands as well as of the small purely mucous glands.

It is a slightly turbid tasteless fluid of a distinctly alkaline reaction, of 1004—1008 specific gravity, and so tenacious that it can be drawn into threads. The amount secreted by an adult human being during 24 hours varies greatly according to circumstances, and has been variously estimated by different authors, by whom the wide limits of 200—2000 grms. (7—70 oz.) have been assigned as the daily amount.

The saliva contains about 5 per cent. of solids. Of these the greater part are organic; namely, (1.) Mucin, from the submaxillary, sublingual, and small mucous glands, which can be precipitated by acetic acid. To this substance the viscidity of the saliva is due. (2.) Traces of albumin precipitable by concentrated nitric acid and boiling. (3.) Traces of globulin, precipitated by carbonic acid. (4.) *Ptyalin*, a peculiar ferment.

The inorganic constituents are salts, among which an inconstant amount of potassium sulpho-cyanate is found, a substance which does not exist in the blood.

There are also many morphological elements, of these the majority are accidental, being the remains of food, &c.; others are more or less characteristic; namely, (1.) Salivary corpuscles which are rounded protoplasmic masses containing nuclei and coarse granules which show Brownian movements. (2.) Epithelial scales from the surface of the mouth. (3.) Various forms of protophyta, which propagate readily amid the decaying particles of food in the mouth. But no bacteria or other fungi exist in the ducts of the glands or saliva taken from the ducts with the necessary aseptic precautions.

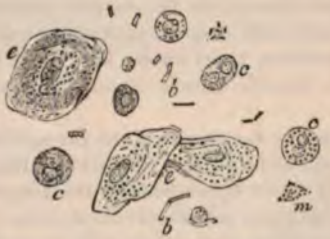


Fig. 63.—The form elements from mixed saliva from tip of tongue, showing (*e*) large irregular scaly epithelial cells, (*c*) round salivary corpuscles, several (*b*) bacteria, and (*m*) micrococci.

The ordinary mixed saliva may be easily collected by chewing some insoluble material, such as a bit of rubber tubing, and collecting the fluid which the motion causes to be poured into the mouth.

The collection of the secretion of the different glands requires more delicate methods. It may be collected separately by placing a canula in the duct of each gland.

The parotid saliva obtained in this way is found to have no structural elements nor mucus, and is a thin fluid dropping easily, and not capable of being drawn into threads. It contains some serum albumin and globulin, potassium sulpho-cyanate, and ptyalin. The portion first secreted is commonly acid, and it never becomes strongly alkaline. Its specific gravity is 1003—1004. On standing it becomes turbid from the precipitation of carbonate of lime, which existed as bicarbonate.

The submaxillary secretion is more strongly alkaline than that of the parotid; it contains structural elements and mucin, but is not so viscid as the general mouth-fluid.

The sublingual is much more viscid than either of the others, and is more strongly alkaline, and contains much mucus and many salivary corpuscles.

THE METHOD OF SECRETION OF SALIVA.—Under ordinary circumstances very little saliva is secreted, only sufficient being poured into the mouth to keep the surface moist. When, however, food is introduced into the mouth, and the process of mastication commences, the secretion goes on more or less rapidly, according to the stimulating or non-stimulating character of the food.

The activity of a salivary gland is at once brought about by means of special nervous agencies when a stimulus is applied to the mouth. We know that the nervous mechanism with which we have here to do, is what is called a reflex act. The stimulus travelling from the surface of the mouth to the nerve centres is reflected thence to the glands. We speak, then, of afferent nerves, which carry the impulses towards the centre, and efferent nerves, which carry them from the centre.

If we review the ordinary circumstances giving rise to a flow of saliva, there will be no difficulty in determining the nerves which act as the afferent channels in the simple reflex act.

Stimulation of the mucous membrane of the tongue and mouth, whether chemically, as with irritating condiments, or mechanically, as by the motions of mastication, is generally transmitted to the centre by the sensory branches of the fifth cranial nerve, which supply the mouth, and by the branches of the glosso-pharyngeal.

The stimulus of the sense of taste is sent by the nerves of that sense, mainly the glosso-pharyngeal, to the taste centre in the cortex cerebri, and from thence to the secreting centre by means of inter-central fibres.

The stimulating of the olfactory region with certain odours induces salivation through a channel of a similar kind passing along the olfactory nerve to the brain, and thence to the special salivary centre. Even in the absence of taste or smell, mental emotion may be excited by seeing or thinking of food, and may cause activity of the salivary glands, here the inter-central channel is the only one occupied in bearing the impulse to the special secreting centre.

Irritation of the gastric mucous membrane stimulates the salivary glands as may be seen with a gastric fistula, or by the sudden flow of saliva which commonly precedes vomiting. In this case the impulses are carried by the gastric branches of the vagus.

The stimulation of the central end of the cut sciatic is said to cause on increase in the flow of saliva, so that it would appear that even an ordinary sensory nerve can excite the centre to action. Lastly, many drugs, when introduced into the blood, cause a flow of saliva, among these are pilocarpin, physostigma, and curara, while atropia and some others, on the other hand, check the action of the glands.

From this we learn that the nerve centre, controlling the activity of the salivary glands, may receive impulses from many distant and diverse nervous sources, or may be influenced directly by the quality of the blood flowing through the special nerve centre itself.

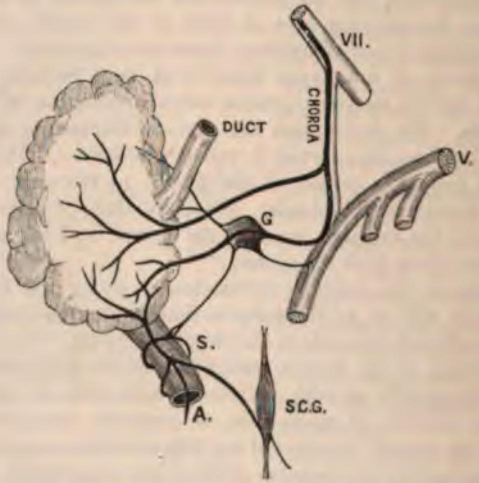


Fig. 64.—Diagram of Nerves of the Submaxillary Gland. The dark lines show the course of the nerves going to the gland.

(VII.) Portio dura; (V.) Inferior maxillary division of the fifth cranial nerve; (G) Submaxillary ganglion; (S) Sympathetic round facial artery (A); (S. C. G.) Superior cervical ganglion.

The channels traversed by the efferent impulses going to the salivary glands have been demonstrated by experiment. In the case of the submaxillary, the route is especially distinct and instructive, so that from this gland we obtain most of our knowledge concerning the direct influence of nerve impulses on the gland cells. This question, therefore, will be treated somewhat in detail.

There are two sets of nerves going to the salivary glands, one belonging to the *sympathetic* and the other to the *cerebro-spinal* systems, both of which have been proved to exert a certain amount of influence on the action of the glands, the share taken by each apparently differing in different animals.

The sympathetic branches for the submaxillary and sublingual gland come from the plexus which embraces the facial artery, those for the parotid come from the plexus surrounding the internal maxillary as that artery traverses the gland. Both of these nervous plexuses are derived from the superior cervical part of the sympathetic nerve.

The cerebro-spinal fibres for the submaxillary and sublingual glands lie in the complex nerve known as the chorda-tympani, which comes from the portio dura of the seventh, and joins the lingual branch of the fifth. They pass thence through the submaxillary ganglion to the glands.

The cerebro-spinal parotid branches pass through the lesser superficial petrosal nerve from the tympanic plexus to the otic ganglion, and thence to the auriculo-temporal nerve which sends twigs to the gland. (Fig. 65.)

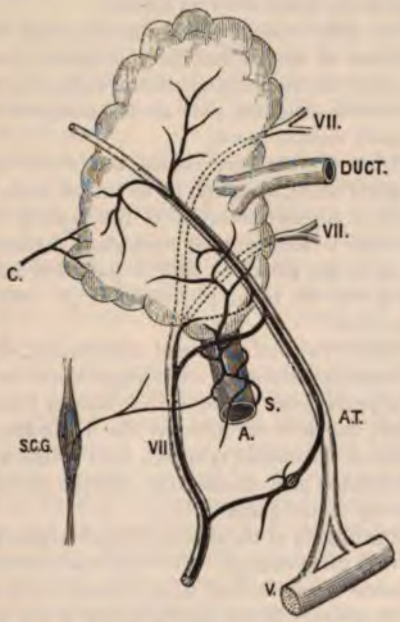


Fig. 65.—Diagram of Nerves supplying the Parotid Gland. The dark lines indicate the course of the nerves of the gland.

(V.) Inferior division of fifth nerve and its (A T) auriculo-temporal branch.
(VII.) Portio dura.
(S. C. G.) Superior cervical ganglion sending a branch to the carotid plexus around the artery.

I.—The effects of experimental stimulation of the *cerebro-spinal* glandular branches, so far as we know are alike for all the glands. But owing to the greater facility with which the submaxillary gland can be reached and its nerve isolated, research has been chiefly devoted to it, by operating on the chorda tympani and the other nerves supplying the gland.

It has been found that section of this nerve, or of the portio dura near its origin, removes the possibility of exciting the glands to action by stimulating the mouth, so that the cerebro-spinal and not the sympathetic are the channels traversed by the reflected impulse on its way to the gland from its centre.

The reflex stimuli which were supposed to be elicited through the medium of the submaxillary ganglion, probably depended on the escape of the stimulating electric current used, and the reflexion from a sporadic ganglion, such as the submaxillary, has never been satisfactorily demonstrated.

It has further been shown that direct stimulation of the chorda tympani nerve, although it be cut off from its central connections, causes a copious secretion of thin watery saliva, and this increased secretion is accompanied by a great dilatation of the small arteries going to the gland, so that a pulsation may be seen in the small veins, and the blood retains its bright arterial colour when leaving the organ.

These two chief results of stimulation, *activity of the secreting cells* and *vascular dilatation*, are brought about by different nerve agencies, as appears from the action of atropia which stops the secretion of saliva, but does not prevent the dilatation of the vessels on stimulation of the chorda tympani, from which we conclude that its effect is restricted to a mechanism engaged exclusively in controlling the activity of the gland cells.

Stimulation of the chorda tympani causes the secretion to be carried on with great energy. The fluid was found to enter the duct with a pressure equal to 200 m.m. (about 8 inches) of mercury, while the blood pressure in the carotid artery of the animal was only 112 m.m. (about 4½ inches) mercury; that is to say, the force by means of which secretion is driven outwards, is nearly twice as great as the pressure in the blood vessels in the gland. The secretion of saliva cannot then be a question of mere filtration, for if the physical agency—pressure—alone were acting, the saliva would be forced into the blood vessels as soon as the pressure in the duct exceeded that in the vessels.

The force and rate with which the secretion is produced vary with the strength of the stimulation. The flow of saliva steadily increases within certain limits as the stimulus gets stronger. It is not only the quantity of the secretion that depends on the amount of nerve impulse, but also its quality; that is to say, with a fresh gland, not wearied by previous experiment, the amount of solids in the saliva increases as the stimulus is increased, so that not only the activity of the gland cells is under the control of nerve influence, but the kind of work they perform is also regulated by the intensity of nerve impulse they receive.

It has been found that the increase in the blood flow is secondary to the secretion called forth by stimulation of the chorda tympani. This is shown by the fact that even when the blood supply is cut off by any means (strong sympathetic stimulation, ligature of the vessels, or even decapitation) an amount of saliva can be made to flow from the gland which could not have been stored up in its cells prior to the stimulation of this nerve.

II.—With regard to the influence exerted by the *sympathetic branches*, the most obvious result of stimulation of these is a contraction in the arterioles, and a consequent diminution of the amount of blood flowing through the gland. The glands look pale, and the blood leaving them is intensely venous in character; the exact opposite, in fact, to the result obtained by stimulation of the cerebro-spinal nerves. But the sympathetic has also an effect on the gland cells, as it produces an increased flow of saliva. In the dog the secretion of "sympathetic saliva" is only temporary and scanty, having high specific gravity, and being overloaded with the solids. In the cat and rabbit "sympathetic saliva" is scanty, and not thicker than the "chorda saliva" of the same animal. So far as regards the blood-vessels, then, the chorda is directly opposed to the sympathetic. To explain this antagonism we may either assume the existence of local nerve centres governing the muscular coats of the arterioles, and suppose that the sympathetic stimulates and the chorda inhibits the activity of these centres, or, what seems more simple, in the absence of anatomical evidence that such a centre exists, we may attribute to the arterial muscle cells themselves an automatic tonic power of contraction which can be increased by the sympathetic and diminished by the chorda tympani. It is singular that if all the nerves leading to the gland be cut, after some hours a pretty copious watery secretion of saliva occurs and lasts for some weeks, after which the cells undergo atrophic changes, and the gland becomes reduced in size. The explanation of the appearance of this so-called "paralytic saliva" is not clearly made out. Possibly the removal of some trophic nerve-influences induces abnormal nutritive changes which cause stimulation of the cells, and ultimately lead to their degeneration.

The histological investigation of the elements of these glands in the various stages of secretion throws considerable light on the behaviour of the cells during their periods of activity and rest.

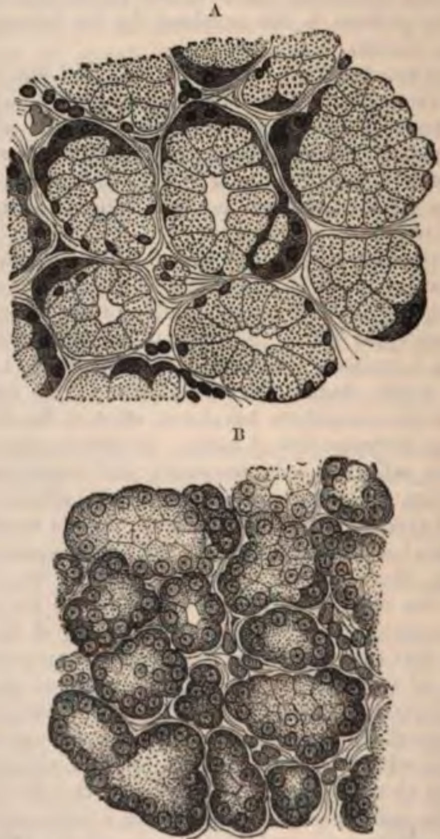


Fig. 66.—Sections of Orbital Gland of the Dog. (Heidenhain.)

(A) After prolonged period of rest. (B) After a period of activity.

In (A) the secreting cells are clear, being swollen up with mucigen, and the half-moon cells are very distinct and darkly stained.

In (B) the accumulated material has been discharged from the cells, and the alveoli are shrunken.

It is now certain that the different stages are accompanied by constant structural changes in the cells, which doubtless are intimately connected with secretory activity. During the period of rest, that is, the time when the gland is not discharging its secretion, the cells slowly undergo a change in their appearance, which is obvious in proportion to the ease with which the material they secrete is recognised in the protoplasm of a cell. Thus, in mucous glands, or in mucus-yielding salivary glands, the changes are conspicuous; whilst in those which give a watery secretion they are less easily seen.

As an example we may take a mucous gland, such as the orbital gland of the dog, and follow the changes which occur in its cell from the time it ceases to discharge its function. (Fig. 66.)

Immediately after the prolonged and active discharge of the secretion of the gland, the cells have all the characters of ordinary protoplasmic units, and the distinction between the polygonal cells and those next the wall of the acinus (demi-lune cells) is made out with great difficulty, because all the cells stain evenly with carmine, and have no special characters except those belonging to active protoplasm.

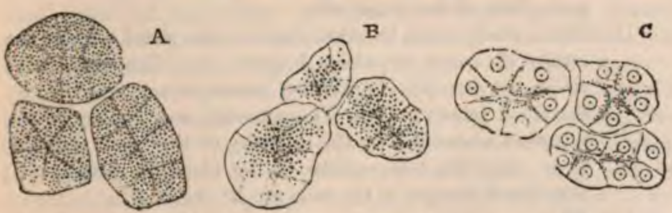


Fig. 67.—Cells of the Alveoli of a Serous or Watery Salivary Gland. (Langley.)

(A) After rest. (B) After a short period of activity.
(C) After prolonged period of activity.

During rest certain changes gradually appear in those gland-cells which are next the lumen of the saccule. They appear to swell towards the lumen, and at the same time become clear and resist staining with carmine, their protoplasm becoming impregnated with mucus-like material (mucigen), while the demi-lune cells remain protoplasmic and stain easily, and are thereby readily distinguished from the cell in the cavity of the saccule.

Now, if the discharge of secretion be called for, either by normal reflex excitation, or by direct stimulus of the chorda tympani nerve, the cells discharge the contained specific material, some of them most probably being destroyed by the act. If the active secretion be continued for some time, the cells return to their former protoplasmic state, and the cells which have been worn out are replaced by others from the demi-lune or marginal cells.

In the glands which do not produce any mucus the brilliant look of the cells after rest is wanting, but a corresponding change occurs. The secreting protoplasm becomes extremely granular during the resting period, and again clear after the discharge of the secretion. (Fig. 67.)

Thus it would appear that during the so-called period of rest, when little or no fluid is poured into the duct, the gland-cells are busy at their manufacturing process, diligently adding to their stock in hand in order to be ready for a sudden demand which they could not meet by merely concurrent work.

To sum up, then, we may conclude :—

I. That the manufacture of the specific materials of the secretion is accomplished as the result of the intrinsic power of the protoplasm of the gland cells.

II. That a vital process is called forth in the gland cells by the action of nerve impulses, because—(1.) The force with which the secretion is expelled cannot be accounted for by the blood pressure. (2.) The quantity and quality of the secretion is modified by the intensity of the nerve stimulation. (3.) The temperature of the blood is raised. (4.) Structural changes in the cells can be observed.

III. The normal stimulus to secretion passes from the centre in the medulla oblongata to the salivary glands along cerebro-spinal, not sympathetic, nerves.

IV. This centre for salivary secretion, which at ordinary times is moderately active, may be excited to energetic action by impulses coming from taste, smell, and ordinary sensory nerve terminals (particularly in the mouth), as well as by those which emanate from mental emotions.

CHANGES UNDERGONE BY THE FOOD IN THE MOUTH.

Food when taken into the mouth undergoes two processes, which are inseparable and simultaneous in action ; viz., *mastication* and *insalivation*.

The mechanism of mastication has already been discussed, so far as its triturating power is concerned. In its final object of forming the subdivided food into a bolus which can be easily swallowed, it is much aided by *insalivation*, particularly in chewing dry food; and in this latter the moistening of the particles, so as to make them adhere together, is the most necessary act of mouth digestion, and is next in importance to the subdivision accomplished by the teeth. Moreover, the saliva covers the bolus with a coating of viscid fluid, so that it can more easily slip down the œsophagus. Deglutition of solids is difficult during a scanty supply of saliva.

Our food is generally composed of materials some of which are soluble in water, and some are not.

While in the mouth the saliva dissolves a great quantity of the more readily soluble materials, such as sugar and salt, which may be either mingled with the insoluble substances, and swallowed together with the bolus, or swallowed separately in a fluid form. Solution, then, is an important item in mouth-digestion.

In many carnivorous animals the use of the mouth-fluid is chiefly mechanical, dissolving some insignificant part of the food, and aiding mastication and deglutition. In man, however, and other animals that make use of much vegetable food, it has a chemical function, and acts on the insoluble starch, converting it into soluble sugar.

The active principle which brings about this change is *Ptyalin.* This is one of a series of ferments which exist in the body, and to which most of the chemical changes in digestion are due. Although each possesses certain peculiarities, yet as a group they may be described as effecting by their presence various alterations in the substances on which they act, while they themselves do not undergo any perceptible change, and a small quantity will do as much work as a larger quantity if allowed a proportionately longer time.

Ptyalin acts exclusively on starch, and hence is spoken of as an amylolytic ferment, its action consisting in causing the starch to unite chemically with one molecule of water thus :—

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + H_2O = \underset{\text{Grape-sugar.}}{C_6H_{12}O_6}$$

During this process, which takes at the least a few minutes to complete, various stages can be detected: first, two substances are formed which together are commonly spoken of as dextrin; one, erythro-dextrin, which gives a red colour with iodine, and easily passes into soluble sugar; and the other, achröo-dextrin, gives no colour with iodine, and is with difficulty converted into sugar. As it gives no colour with the ordinary test, its presence is often overlooked.

The sugar thus formed has been called *Ptyalose*, which, however, can be converted into ordinary grape sugar (glucose) by the action of sulphuric acid. Some say the product is all maltose.

The presence of starch, either in its soluble or insoluble form, is easily recognised by the blue colour given by free iodine, which colour disappears on heating to about 100° C., but reappears on cooling.

Very many tests have been recommended for the detection of sugar. The most generally applicable one is Trommer's. The liquid is made strongly alkaline with potash, and a few drops of a dilute solution of cupric sulphate is added, a clear blue solution results, which, on being raised to the boiling point, deposits a yellow precipitate of cuprous oxide. Fehling's and Pavy's solutions are modifications of the above test adapted for quantitative analysis.

When yeast is added to grape-sugar and placed in an inverted test-tube, the sugar is converted into alcohol and carbon dioxide. The latter rises to the top of the test-tube, and can be used as an indication of the quantity present. Experiments may be carried out with saliva obtained from any of the glands directly, but the mixture of the secretion of all is found to be more efficacious than that of any single one. The ordinary mouth-fluid filtered serves well for ordinary experiment.

An effective glycerine solution of ptyalin may be obtained by steeping chopped salivary glands in alcohol, and then extracting for some days with glycerine and water.

The following facts must be borne in mind concerning the amylolytic action of ptyalin:—

1. The extremely small amount of the ferment required to make the fluid effective.
2. There is no appreciable diminution in the amount of ferment, so that it cannot be said to be used up in the process.
3. The action takes place most readily in alkaline solutions, such as the saliva, slowly in neutral solution, and not at all in acids of the strength of ·2 per cent. of hydrochloric acid.
4. Temperature has a marked effect on the process. Cold (0° C.), quite checks the action; heat (75° C.) destroys the power of the ferment, which is most active at the body temperature (35°—40° C.).
5. Strong acids or alkalies destroy the amylolytic power of ptyalin.
6. The ferment has but little effect on raw starch, its cellulose

coating protecting it; but it acts rapidly on well-boiled starch.

7. Ptyalin is more active in weak solutions, and seems to be impeded in its action by an accumulation of sugar.

To recapitulate, we find that the following changes take place in the mouth :—

(1) Solid food is or should be finely subdivided; (2) dry food is moistened, (3) rolled into a bolus, (4) and lubricated; (5) the soluble part is dissolved, and rendered capable of being tasted; (6) and part of the starch is converted into soluble sugar by the action of a ferment called *ptyalin*.

In the short time occupied by the passage of food through the œsophagus no special change takes place in it, so we may pass on at once to the gastric digestion, which will occupy the next chapter.

CHAPTER VIII.

STOMACH DIGESTION.

The general surface of the stomach is covered by a single layer of cylindrical epithelial cells which also line the orifices of the numerous glands with which the mucous membrane is thickly studded. This single layer of cylindrical cells is marked off from the stratified squamous cells lining the œsophagus by a sharp line of demarcation. The glands of the stomach are tubes of which the orifices are conical depressions which divide into two or three tubular prolongations. The outlet or orifice is covered by the common cylindrical epithelium of the surface of the stomach, and the fundus is filled with specific granular cells. The glands dip down into the delicate submucous tissue, the branching tubes lying parallel and exceedingly close together. Between them an injection demonstrates a dense network of capillary vessels which surrounds the tube and closely invests the delicate basement membrane which forms the boundary of the glands and the basis of attachment of the glandular cells.

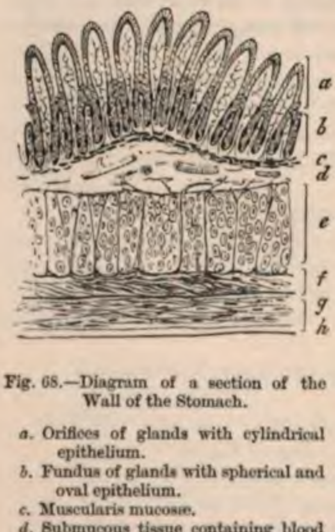


Fig. 68.—Diagram of a section of the Wall of the Stomach.

- *a*. Orifices of glands with cylindrical epithelium.
- *b*. Fundus of glands with spherical and oval epithelium.
- *c*. Muscularis mucosæ.
- *d*. Submucous tissue containing blood vessels, &c.
- *e*. Circular, (*f*) oblique, and (*g*) longitudinal muscle coats.
- *h*. Serous membrane.

In the cardiac end of the stomach two distinct kinds of cells are found in the deeper part of the gland tubes. One kind, which is much the more numerous, consists of small pale spheroidal cells, which occupies the lumen of the gland and forms the regular cell-lining of its cavity. These cells have been called the "chief cells" (Hauptzellen), or "central *spheroidal cells.*"

The cells of the other form are comparatively few, being altogether wanting in some of the glands. They are larger and more striking than the central cells between which and the basement membrane they lie scattered here and there over the fundus of the gland, making the delicate membrane bulge. They stain more easily, and have darker granules than the central cells. On account of their position they have been called "parietal," "marginal or border cells" (Belegzellen), and from their oval shape, which equally well distinguishes them from the other, "*ovoid cells.*" (See fig. 69).

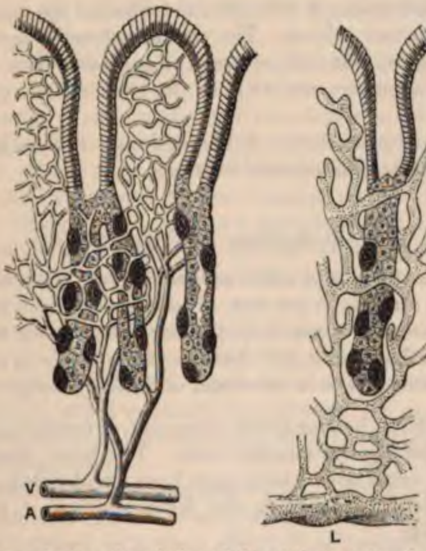


Fig. 69.—Diagram showing the relation of the ultimate twigs of the blood-vessels (V and A), and of the absorbent radicals to the glands of the stomach and the different kinds of epithelium, viz., above cylindrical cells; small pale cells in the lumen, outside which are the dark ovoid cells.

There is a different class of glands, the so-called mucous, found chiefly near the pyloric end of the stomach, in which there is but one kind of cell throughout, and this seems to differ in character from both the varieties in the other glands, resembling rather the cylindrical epithelium covering the surface of the stomach and dipping into the conical orifices which lead to the glands.

The difference between the two kinds of glands found in the stomach, both as regards their distribution and way of branching, and the cells which line the deeper parts of the tubes, is found to vary in different animals. The difficulty of obtaining fresh specimens of the human stomach makes it still uncertain whether the same differences exist in the human subject. The varieties of opinion and drawings published suggest that various stages of gradation from one kind of gland to another are met with in the stomach of even the same animal.

Experimental research does not show decisively that the anatomical differences denote differences of function.

THE CHARACTERS OF GASTRIC JUICE.

THE gastric juice is a clear colourless fluid with strongly acid reaction. It contains ·5 per cent. of solids, its specific gravity being 1002. The amount secreted in the day is extremely variable, and depends upon the amount and character of the food ; in well-fed dogs it has been estimated to be one-tenth of the body weight.

1. It contains, in man, about ·2 per cent. of free hydrochloric acid, in the dog considerably more. The lactic, formic, butyric, and other acids which have been found in the gastric juice probably depend on the decomposition of some of the ingesta.
2. Pepsin, the specific substance which gives the gastric juice its digestive qualities, is a nitrogenous ferment which, with the foregoing acid, acts on proteids. About ·3 per cent. is present in the secretion of the human stomach. It is probably associated with other less known ferments, one of which curdles milk without the presence of any acid.
3. A variable quantity of mucus is found in the secretion of the stomach.
4. It contains ·2 per cent. of inorganic salts, chiefly chlorides of sodium, potassium and calcium.

METHOD OF OBTAINING GASTRIC SECRETION.—Formerly attempts were made to obtain gastric juice by obliging a dog while fasting, to swallow a sponge, and withdrawing it when saturated with the gastric secretion ; or a fasting dog, allowed to swallow insoluble materials, was killed, and the secretion produced was collected from the stomach. It is best obtained directly from a fistulous opening in the abdominal wall communicating with the stomach.

A gastric fistula was first made by accident. It was a case in which the surgical treatment of a gunshot wound of the stomach of a man left a permanent fistula, by means of which the gastric secretion was carefully investigated. Thus a man proved a valuable subject for experimental research.

It is not a difficult matter to reach the stomach by making an artificial opening through the wall of the abdomen, and, having brought the serous surface of the gastric wall into firm connection with the serous lining of the abdominal wall, to open the stomach. The juxtaposition of the parts as well as the patency of the fistula can be secured by a suitable flanged cannula closed with a well-fitting cork. By removing the cork the gastric juice may be obtained in small quantities, and various kinds of food may be introduced through the cannula, and the changes occurring in them studied.

For experimental purposes an artificial gastric juice may be used. This can be made from the gastric mucous membrane of a dead animal (pig) by extracting the pepsin from the finely divided glandular membrane, with a weak acid (less than ·2 per cent.), or better with a large quantity of glycerine, and subsequently adding HCl to the extent of ·2 per cent.

Mode of Secretion.—The gastric juice is not secreted in large quantity when the stomach is empty, but only when the mucous membrane is irritated with some chemical or mechanical stimulus. The swallowing of alkaline saliva acts as a gentle stimulus and causes secretion, so that the surface of the stomach becomes acid. When the lining membrane of the stomach is mechanically stimulated through a fistula it becomes red, and drops of secretion appear at the point of stimulation, but the amount of secretion thus produced is very scanty when compared with that called forth by chemical irritants.

Thus ether, alcohol, and pungent condiments produce copious secretion. Weak alkaline solutions also cause secretion, but the most perfect form of stimulant seems to be the normal one, namely, a consistent mass of food saturated with the alkaline saliva.

In all probability the secretion of the gastric juice is under the control of a special nerve mechanism, and the way in which the state of activity follows stimulation of the part seems to point to its being a simple reflex act. However the nervous connections (vagi and splanchnics) between the stomach and central nervous system may all be severed without any marked effect on the secretion, other than that which would naturally follow the changes in the amount of blood supply, which of course is profoundly altered by cutting the vaso-motor nerves—the splanchnics. Whether this be so or not, there must be some connection with the nerve centres, for sudden emotions check the secretions, and the sensations caused by the sight or smell of food give rise to gastric secretion.

It has been suggested that Meissner's sub-mucous ganglionic network may act as a reflex centre and regulate the secretion. But since reflection from local ganglionic centres has not yet been definitely demonstrated, we are hardly entitled to assume that it occurs here, and since the stimulus comes into close contiguity with the secreting cells, it seems quite as probable that these elements are excited to activity by direct stimulation of their protoplasm.

As in the salivary glands, so in the gastric tubes, the cells show some structural changes which accompany with great regularity their periods of rest and activity, and therefore may be concluded to be the indications of the internal processes belonging to the production of the specific materials of their secretion.

It appears probable that the chief secretory activity resides in the small central cells, and not in the large ovoid border-cells, since no distinct changes can be seen in the latter, and the smaller gland cells seem to contain the pepsin, for if the mucous membrane be treated with weak hydrochloric acid, these central gland-cells are rapidly dissolved by a process of digestion, while the border-cells simply swell up and become more transparent. So that the outer ovoid cells have no title to their former name of "peptic cells."

The central cells of the gastric glands are finely granular, pale, protoplasmic masses, and continue so during the time when the stomach is empty and the glands not secreting. In the earlier stages of digestion these cells swell up and become turbid and coarsely granular, and stain more readily with the aniline dyes. As the digestive process goes on the cells again diminish in size, but are found to contain a large quantity of peculiar granules, which are discharged from the cell before its return to the ordinary state of rest. The cells are said to be rich in pepsin in proportion to their size; when swollen during active digestion they contain much pepsin, when small, during hunger, they contain but little.

It would therefore appear that the pepsin of the gastric juice is produced as a distinct and new manufacture by the central cells of the peptic glands, and not by the other cells. Structural changes have also been followed out in the so-called mucous glands and in glands without any of the ovoid border-cells, which, taken with the fact that the alkaline secretion of the pyloric end of the stomach, where the mucous glands abound, is capable of rapidly digesting proteid if acid be added to it, tends to show that in these so-called mucous glands pepsin is also produced.

The acid is found chiefly on the surface of the stomach. The mode of its production seems distinct from that of pepsin, but is not well understood. Although the deeper part of the glands do not give an acid reaction, while the neck and orifices of the gland are distinctly acid, there is good reason for believing that this manufacture of acid from the alkaline blood is really an active process carried out by some glandular cells.

It has been suggested that the cell elements which produce the acid are the ovoid border-cells, from whence it rapidly passes to the orifice of the glands. This view is supported by the alkalinity of the pyloric end of the stomach where the border cells are not found. In some animals the distinct distribution of the different cell elements and the accompanying reaction of the secretion are well marked.

ACTION OF THE GASTRIC JUICE.

The gastric juice has in the absence of mucus no effect on the carbohydrates, and probably the amylolytic fermentation set up by the saliva is impeded, if not completely checked, by the free acid in the stomach.

The gastric juice has no effect on pure fats, but it dissolves the proteid frame-work of adipose tissue and thus sets the fats free, which are then turned by heat to a liquid mass like oil. Upon the albuminous bodies the gastric digestion produces a marked effect. The proteids being colloid bodies cannot pass through an animal membrane by the process called dialysis; it has therefore been assumed that they cannot be absorbed through the lining membrane of the stomach. They are also often eaten in an insoluble form. To convert the insoluble and indiffusible albumins into a soluble and diffusable substance would obviously be a great step towards their absorption. This power is ascribed to the gastric juice. The steps of the process may be accurately followed in a suitable glass vessel, irrespective of the stomach, by using artificial gastric juice, and attending to the various conditions necessary for its action. The power of artificial gastric juice carefully prepared from the mucous membrane of an animal's stomach differs in no essential respect from that of the natural secretion in the stomach, if all the circumstances which aid the action of the gastric ferments be applied in the experiment. This action consists in a conversion of coagulated albumins into the peculiar soluble and diffusible form of proteid known as "peptones."

The change is not effected immediately, but certain stages may be recognised in which the two chief constituents of the gastric juice, the acid and the pepsin, seem to have a separate action.

Shortly after the introduction of a proteid, such as boiled fibrin, into gastric fluid at the temperature of the body, the masses of fibrin swell up, become transparent and eventually are easily shaken to pieces and dissolved.

The first step in the process seems to be brought about by the free acid, and consists in the formation of *acid albumin*. This can be shown by neutralizing the fluid during the process and thereby causing a precipitate of acid albumin (v. p. 39). The amount of this precipitate will depend upon how far the conversion into peptone—which is not precipitated by neutralization—has progressed. Thus, in the earlier stages, nearly all the proteid used will be thrown down by neutralization, while only a comparatively small amount is precipitated in the later stages.

The formation of acid albumin may be effected with acid alone without the other constituents of the gastric juice, and therefore the preliminary step may be attributed to the unaided action of the acid; but since this stage in the formation of peptone is constant, and the material may possibly be distinguishable from the ordinary acid albumin, it has been called *parapeptone*.

While the parapeptone is being formed by the acid, the pepsin is engaged in changing it into the final soluble, diffusible and uncoagulable product—peptone. The pepsin by itself cannot convert proteid into peptone, as may be seen in the want of efficacy of a neutral solution of pepsin, in which neither peptone nor parapeptone is formed. In other words, pepsin solution can only change parapeptone or acid albumin into peptone. It would appear probable, however, that it possesses this property to an unlimited extent, since it undergoes no change itself, and with fresh supplies of acid a very minute quantity of pepsin can convert an indefinite amount of proteid into peptone.

The rapidity with which proteid is converted varies according to the circumstances under which it is placed as well as the kind of proteid used. If the same proteid be used the following circumstances will be found to influence the rapidity of the process :—

1. The temperature. As already stated, the *optimum* degree of heat for the change is about that of the body, 30° F.—40° C. The activity of the gastric juice diminishes when the temperature either rises above or falls below this standard. The minimum at which it is capable of action at all is about 1° C. and the maximum is about 90° C. Boiling permanently destroys the function of pepsin.
2. The percentage of acid as well as the kind of acid has a marked effect. Though the action will go on with other acids, Hydrochloric is the most effective, and that of a strength of ·2 per cent.
3. Large quantities of salts in solution or a condensed solution of peptone impede the process, a certain degree of dilution being necessary for the process. In strong solutions of proteid, the peptones must be removed by dialysis in order to allow of the continuance of the action. This occurs in the stomach by means of the blood and absorbent vessels.
4. The degree of subdivision to which the proteid has been subjected materially influences the rapidity of its conversion into peptone. The more finely subdivided the substance the greater will be the relative extent of surface exposed to the action of the digestive fluids. When large masses are introduced into the stomach, the gastric fluid cannot reach the central portions, and their digestion must await the completion of that of the exterior part.
5. Motion aids the action of the foregoing factors.

All these requisites are found in the normal act of digestion. The temperature of the stomach is 38° to 39° C. (= 100° F.). Hydrochloric acid is present in the proportion of about ·2 per cent. : as quickly as the peptones are formed they can be removed by absorption from the stomach, and thus the needful dilution is accomplished : and finally, if the mouth has done its duty, the pieces of proteid have been reduced to a pulp, composed of minute particles : these are kept in constant motion by the gastric walls, and thus are repeatedly brought in contact with fresh supplies of the digestive fluid.

There can be little doubt that the conversion of proteid into peptone is normally brought about by the pepsin, which acts as a ferment, in some way or other facilitating a process which without it is extremely difficult to accomplish. Proteids may, however, give rise to peptone without the presence of any pepsin at all, if they be treated with strong acids, alkalies, boiling under high pressure, putrefactive and other fermentative actions. This, together with the analogy suggested by the chemical details of the amylolytic action of saliva, which one may say depends on an atom of water being taken up, suggests that the change of proteid into peptone is also hydrolytic, the peptones being simply an extremely hydrated form of proteid.[*]

So far we have found that the action of the gastric juice affects proteids alone. Its action on other constituents of food varies. *Gelatinous* material is dissolved by the gastric digestion and rendered incapable of forming a jelly; its conversion into peptone has, however, not been established. The connective tissue of meat is therefore soon removed, and the muscle fibres fall asunder, the sarcolemma is dissolved, and the muscle substance is converted into true peptone. The delicate sheets of elastic tissue, such as basement membranes and those of small vessels, are dissolved, but larger masses of yellow elastic tissue are not affected by the gastric digestion. The horny part of the epidermis, hairs, &c., are quite unaltered, and also the mucus, which passes along the alimentary tract without change. Bone dissolves slowly, the animal part being attacked at the surface by the gastric juice and the acid slowly removing the salts.

The action of the gastric juice on *milk* is peculiar. On reaching the stomach milk is curdled by a special ferment formed in the gastric mucous membrane. This is known as "Rennet," which is made from the stomach of the calf, and used in the manufacture of cheese. The precipitation of the Casein (alkali albumin), which gives rise to the curdling of the milk, is not brought about by the hydrochloric acid (although the acidity would be sufficient cause), because neutralized gastric juice has the same effect. It appears that a special ferment (not pepsin) which directly affects the casein and causes its coagulation, must exist. It is not due to common lactic ferment, for though lactic acid is produced, it is formed too slowly to account for the very rapid coagulation of milk which occurs in the stomach.

---

[*] Though proteids will not diffuse through a dead animal-membrane when distilled water is used, a fair amount of diffusion takes place if a suitable solution of common salt be employed instead of water. It must also be remembered that the gastric mucous membrane is a living active structure, and that the fluid into which the albumins have to diffuse may be regarded as a salt solution. It is therefore quite probable that a considerable quantity of albumin may be absorbed as such. The fact that peptone cannot be found in any quantity in chyle or portal blood tends to prove that the albumin does pass through the stomach wall without being changed into peptone.

The gastric juice has little effect on vegetable food in general, though well-masticated bread may be very materially altered, owing to the action of the saliva on the starch continuing until the mass is broken up, and the gastric juice then dissolving the proteids (gluten). The greater part of the substance of bread, however, leaves the stomach in an imperfectly digested state.

In short, the amount of change which any given form of food will undergo in the stomach will depend on the amount and exposed condition of the proteid it contains.

In recapitulating the chief events of gastric digestion, it must be remembered that while the food is yet in the mouth the secretion of the gastric juice commences, and is greatly increased by the arrival of a bolus of food and a quantity of frothy alkaline saliva. As the stomach is filled, more and more secretion is produced, and as some food is absorbed an additional stimulus is applied. Being kept in motion in a large quantity of liquid which dissolves the cases in which the food particles are contained, the bolus of food soon falls asunder and each of its ingredients is fully exposed to the action of the gastric juice. The acid reaction of the gastric fluid neutralizes the alkalinity of the saliva, so that the action of the ptyalin is hindered, and the starch granules float about quite unaffected by the pepsin or hydrochloric acid. The heat of the stomach melts the fats, and the motion breaks up the oily fluid into smaller masses. They are then mingled with the general fluid, which becomes more and more turbid owing to the admixture of starch granules, fat globules, dissolved parapeptones, and minute particles of partially digested proteids. This dull grey turbid fluid is called *chyme*. The proteids (which class of food-stuffs are most profoundly affected by the gastric digestion) are changed more or less rapidly according as their particles are small and uncovered, or large and massed together, so that they are more or less readily reached by the gastric juice, and also in proportion to the facility with which they form acid albumin. The chyme contains but little peptone, so that we may conclude that, when formed, it is rapidly absorbed as are also the soluble sugar and ordinary fluids taken with the food. The chyme begins to leave the pylorus soon after gastric digestion has begun, some passing into the duodenum in about half an hour. The materials which resist the gastric secretion, or are affected very slowly by it, are retained many hours in the stomach, and the pylorus may refuse exit to such materials for an indefinite time, so that after causing much uneasiness they are finally removed by vomiting. However, many solid masses, un-chewed vegetables, &c., escape through the pylorus when it opens to let out the chyme.

CHAPTER IX.

PANCREATIC JUICE.

Second only to the stomach in importance as a digestive cavity, is the duodenum, into which the copious secretion of two of the largest glands of the body—the pancreas and the liver—is poured.

The pancreas is a large compound sacculated or acinous gland, being composed of numerous irregular packets of gland tissue attached by its lateral branchlets to the main central duct. The saccules are rather elongated, but have the same general construction as those of the serous salivary glands already described. A single layer of irregular or slightly conical cylindrical cells in the saccule, shows a difference of structure in its central and peripheral sides, so that an external or homogeneous zone, and an internal granular zone may be distinguished. Each zone corresponds to one half of the cells, the clear half being next the boundary, and the granular half next the lumen of the saccule. The relative width of these zones varies with the digestive process, so that the nuclei which are situated between them sometimes appear to be in the outer clear zone, and sometimes in the inner granular zone. The outer zone colours readily with carmine, whilst the inner zone remains unstained.

The large duct which passes down the axis of the gland, receiving tributaries on all sides, is surrounded with a layer of loose connective tissue which forms an outer coat. The proper coat of the duct is composed of elastic tissue, lined by a single layer of cylindrical epithelium.

Collection of Pancreatic Juice.—From a temporary fistula the secretion of the pancreas can be obtained in sufficient quantity to determine its character and properties. A permanent fistula is established with difficulty, and the secretion soon alters its characters, becoming thin and losing its efficacy, most probably being altered by an abnormal state of the gland.

An artificial pancreatic juice may be extracted by water from the minced gland taken a few hours after death from an animal which has been killed during active digestion (a couple of hours after eating). This extract, used with proper precautions, will have the same effect as the secretion itself.

A glycerine solution containing the active principles of the pancreatic secretion may also be made from the pancreas of a dead animal by treating the minced gland for a couple of days with absolute alcohol, removing the alcohol, and substituting sufficient glycerine to cover it, in which it should remain a week or so. This extract, filtered, contains but little else than pancreatic ferments.

Characters of the Secretion.—The pancreatic juice is a very thick transparent, colourless, strongly alkaline fluid, which turns to a jelly if cooled to 0° C. It often contains about ten per cent. of solids when obtained from a temporary fistula, but it may have as little as two per cent.

Of these a considerable proportion are organic, namely :—

1. Albumin which is coagulated by boiling.
2. Alkali albumin, precipitated by acetic acid or by adding magnesium sulphate to saturation.
3. Leucin and tyrosin.
4. Fats and soaps.
5. Salts, particularly sodium carbonate, which makes it alkaline.
6. Three ferments, to which it owes its specific action on the food-stuffs.

Mode of Secretion.—The pancreas does not continue in a state of activity during the interval between the periods of active digestion. When the gland is at rest it is of a pale yellow colour and is flaccid, but during active digestion it becomes more turgid, and assumes a pinkish colour from the increased flow of blood. The secretion commences immediately after taking food, and rises rapidly for a couple of hours, then falls and rises again in the later hours of digestion, five to seven hours after a meal ; then it gradually falls for eight to ten hours, and ceases completely when digestion is at an end. The first rise which accompanies the introduction of food into the stomach, is certainly brought about by nervous agencies of a similar nature to that of the stomach, the secretion of which follows closely upon mastication. The second accompanies the passage of the undigested food through the small intestines, and may also be most conveniently explained as the result of reflex nervous stimulation of the gland cells.

The great complexity of the nerve distribution to the glands of the intestinal tract makes it difficult to ascertain the exact channels traversed by the afferent and efferent impulses. The following observations, if accurate, would tend to prove that certain inhibitory impulses pass from the stomach along the vagus to the medulla, and are thence reflected to the gland by its vaso-motor nerves. During vomiting, or when the central end of the divided vagus is stimulated, the secretion of the pancreas ceases. Section of the nerves which surround the blood vessels distributed to the pancreas causes considerable (paralytic) flow of secretion which stimulation of the vagus cannot check.

No nerve channels have been demonstated to carry exciting impulses direct to the glands, as the chorda tympani does to the submaxillary; but the direct stimulation of the gland itself, or of the medulla oblongata, is said to induce activity of the gland.

During the period of rest of the pancreas, *i.e.*, when the alimentary tract is not in activity, no secretion flowing from the duct and the gland being pale, the gland cells in the acini undergo a change which may be compared with that observed in the cells of the serous salivary glands. The division of the row of cells lining the acinus, into a central granular and outer clear zone, has already been mentioned.

Immediately after very active secretion, the central granular zone is reduced to a minimum owing to the paucity of granules; and the outer zone occupies the greater part of the cell, the entire substance of which stains readily and looks like ordinary protoplasm. After rest, however, the granules re-appear, and after the lapse of a short quiescent period, the inner granular zone has again encroached on the outer, owing to the accumulation of granules which, rapidly increasing, fill the greater part of the cells, and cause them to bulge inwards and occlude the lumen of the gland. When digestion commences, the cells undergo a slight change in form, so that each individual cell is more distinctly seen, and its angles are retracted, giving a notched appearance to the margin of the acinus. The blood supply during this period is much increased, red arterial blood flowing from the veinlets of the gland. At the same time the granules are diminished in number, escaping at the free central margin of the cells into the lumen towards which they appear to crowd, leaving the outer zone once more clear and free from granules, while the lumen of the saccule and of the ducts are filled with secretion.

Let us then examine a single cell; during the period of rest with a comparatively poor supply of blood, the cell receives its normal nutrition, which is accompanied by an accumulation of granules in the protoplasm next the free side of the cell. During secretion these granules are pushed out of the cell, and seem in some way to form the secretion.

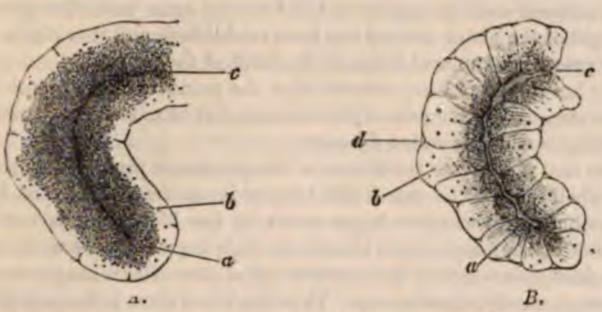


Fig. 70.—One Saccule of the Pancreas of the Rabbit in different states of activity.

A. After a period of rest, in which case the outlines of the cells are indistinct, and the inner zone, *i.e.*, the part of the cells (*a*) next the lumen (*c*), is broad and filled with fine granules.

B. After the gland has poured out its secretion, when the cell outlines (*d*) are clearer, the granular zone (*a*) is smaller, and the clear outer zone is wider. (Kühne and Lea.)

It will be seen immediately that one of the most important functions of the pancreatic juice is the formation of peptone from proteid, which operation is carried out by a special ferment called *trypsin*. It has been found that this ferment can only be obtained from the active pancreas, and that the wider the inner granular zone of the cells is, the richer in ferment is the glycerine extract made from the gland. But it has also been found that if a glycerine extract be rapidly made from an actively secreting absolutely fresh gland, *i.e.*, removed from the dead animal while still warm, the extract is found to be quite inert towards proteids, while an extract made from a portion of the same pancreas which has been kept some hours after death is very active; and a portion of the fresh pancreas pounded in a mortar with a little weak acid so as to develop the trypsin in it, acts in an alkaline solution and forms peptone energetically.

as an example. Olein is a compound of oleic acid and glycerine. Olein in presence of ferment and soda gives glycerine and oleic acid, and the latter combines with soda to form soap. This process materially aids in the next. (II.) Emulsification.—Which means that the fat is reduced to a state of very fine sub-division, as it exists in milk. The production of this condition is facilitated by (1), the quantity of albumin in solution; (2), the alkalinity of the fluid; (3), the presence of soap alluded to above; and (4), the motion of the intestines.

III. *Action on Starch.*—This action of the pancreatic juice seems to depend on a separate ferment (*Amylopsin*), and with the exception that it is much more rapid and energetic, and is said to affect raw as well as boiled starch, its action seems to be identical with that of the saliva. This power is found to exist in the extract of the gland, whether it has been removed from a fasting or from a recently fed animal, and therefore does not depend on whether the gland is engaged in active secretion or not.

CHAPTER X.

BILE.

The liver has two chief functions, which are so distinct in their ultimate object that they may be conveniently described separately, although we are not aware that any natural distinction exists in the manner of their performance. One is mainly excrementitious, namely, the secretion of bile,* which belongs to the fluids connected with digestion, and therefore naturally falls into this chapter. The other is purely nutritive, consisting in the formation of glycogen. The glycogenic function of the liver is of the first importance in the elaboration of the blood, and will therefore be reserved for the chapter on that subject.

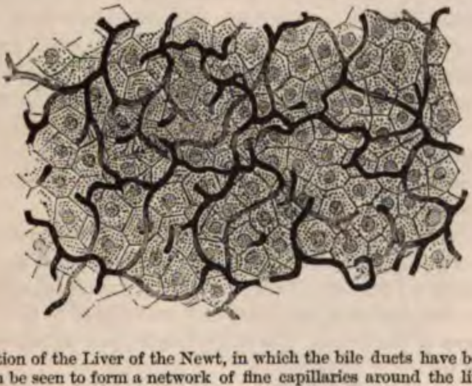


Fig. 71.—Section of the Liver of the Newt, in which the bile ducts have been injected, and can be seen to form a network of fine capillaries around the liver cells, the outlines and nuclei of which can be seen.

---

* Probably also the manufacture of urea should be mentioned here, for there is no doubt, as will be seen later on, that the liver has an important share in producing this substance.

Among the most striking anatomical peculiarities of the liver are: (1) The gall bladder is its receptacle for storing the secretion until it is required. (2) It has a double supply of blood. Besides that coming from the spleen, pancreas and intestinal canal, collected by the tributaries of the great portal vein, and distributed by its branches to the liver, it receives by the hepatic artery a small supply of fresh arterial blood. (3) A beautiful network is formed by the minute ducts (bile capillaries) which freely anastomose between the cells. (4) Although in the embryo, and in many animals throughout their adult life, the liver is a compound saccular gland, yet the relation of the duct radicles to the saccules is so modified in the higher animal and man, that the analogy is no longer apparent, and the structural arrangement is best understood by following its vascular groundwork.

STRUCTURE OF THE LIVER.—On the surface of the liver are seen small rounded markings about the size of a pin's head, which give the organ a peculiar mottled appearance. This is much more striking in some animals (giraffe, bear, pig) than others, but easily recognizable in the livers of all mammalia. These little areas mark out the *lobules* of the liver. They are surrounded by a dark red boundary, and their centre is marked by a dark spot, between which there is a paler yellowish zone. The dark parts correspond to the blood-vessels, and have a constant relation to the lobules.

The entire liver is made up of these little lobules, and each one of them has the same construction and blood supply, and therefore forms in itself a little liver perfect in all its structural arrangements, so that the description of one such unit will suffice to give an idea of the structure of the liver. For other details, anatomical works must be referred to.

The branches of the large portal vein and those of the small hepatic artery pursue the same course through the gland, and are enclosed in a sheath of connective tissue, which also forms the bed of the hepatic duct and its numerous tributaries. If these branching vessels be followed to their final ramifications, they are found to pass around and between the neighbouring lobules. The branches of the portal vein in this situation receive the name of the *interlobular veins.* They anastomose freely with the terminal veinlets in the vicinity, so as to form a network round each lobule. From this a number of capillary vessels pass into the lobule, and, lying between the gland-cells form a network with long meshes radiating from the centre like the threads of a spider's web. These are the *lobular blood capillaries*.

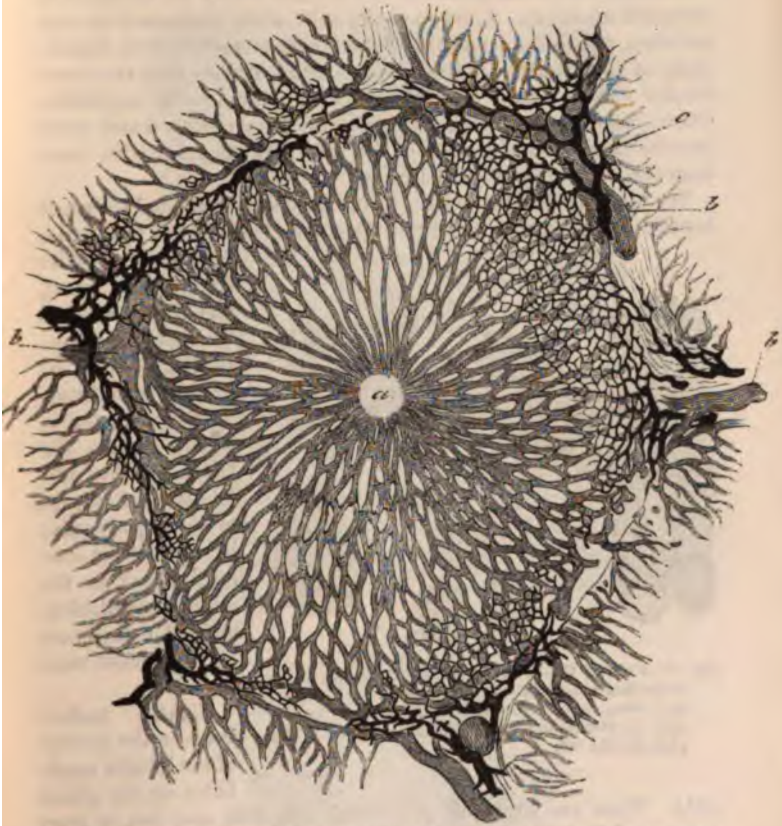


Fig. 72.—Section of Lobule of Liver of Rabbit in which the blood and bile capillaries have been injected. (Cadiat.)

a. Intralobular vein. *b*. Interlobular veins.
c. Biliary canals beginning in fine capillaries.

The vessels of this radiated capillary network become larger as they unite and converge to the centre of the lobule, where they open into a central vein which lies in immediate apposition with the gland cells. This vein is called the *intralobular vein*, and is the radicle of

Between the cells of the lobules there can be demonstrated very fine straight anastomosing canals, which appear to be formed by the juxtaposition of grooves which lie in the middle of the flat surface of two neighbouring cells. Every liver cell is related to such a canal, and consequently a very dense network with peculiarly regular polygonal meshes is present, each mesh corresponding in size to one cell.

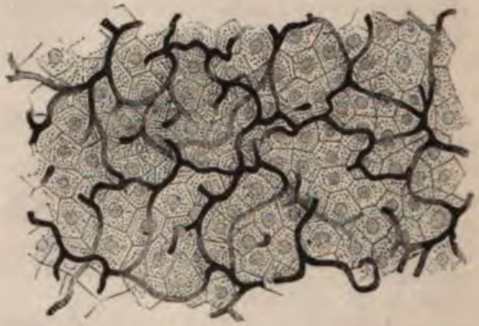


Fig. 75.—Section of the Liver of the Newt, in which the bile ducts have been injected, and can be seen to form a network of fine capillaries around the liver cells, the outlines and nuclei of which can be seen.

These fine intercellular canals are called *lobular bile capillaries*, and must not be confounded with *lobular blood capillaries*, the diameter of which is about ten times as great as the former, and which have a definite boundary wall, whilst the bile capillaries have no other boundary than the substance of the liver cell, and therefore are not really vessels.

These fine intercellular bile passages are described as communicating with the interlobular ducts directly opening into the ducts without any marked increase in the size or change of arrangement. The interlobular ducts which follow the course of the artery and portal vein are composed of a delicate basement membrane lined with a thin layer of epithelium which in the larger vessels shows a cylindrical character. The larger bile ducts have a firm fibro-elastic coat lined with a definite mucous membrane covered with cylindrical epithelium lying upon a vascular submucosa, in which are scattered numerous glands of saccular form.

The amount of connective tissue in the liver of man and most domestic animals is very small, but in the pig, bear, giraffe, and some others, it is easily recognised around the lobules, sending delicate supporting processes between the cells of the lobules. It passes into the organ with the portal system of vessels forming a loose sheath derived from the capsule of Glisson, and is distributed with the subdivisions of those vessels to the various parts of the gland.

The lymphatics are known to be very plentiful, and in intimate relation to the blood-vessels.

METHOD OF OBTAINING BILE.—For most practical purposes the bile obtainable from the gall-bladder of dead animals is sufficient. The bile pigments and cholesterin may be conveniently obtained from the gall-stones so often found in the human gall-bladder.

In order to investigate the composition of the bile as it comes from the ducts, before it has been modified by its sojourn in the gall-bladder, it is necessary to make a biliary fistula, communicating either with the gall-bladder or with the bile-duct. In this way the rate, pressure, and other points concerning the mode of secretion may be determined.

COMPOSITION OF BILE.—The bile of man and carnivorous animals is of a deep orange-red colour, turning to greenish-brown by decomposition of its colouring matter. In herbivorous animals it has some shade of green when quite fresh, but turns to a muddy brown after a time. It is transparent, and more or less viscid according to the length of time it has remained in the gall-bladder. It has a strong bitter taste, a peculiar aromatic odour, and, after remaining for some time in the gall-bladder it has an alkaline reaction. Its specific gravity is about 1010 when taken from the bile-ducts directly, but it rises to 1030 after prolonged stay in the gall-bladder, owing to the addition of mucus and the absorption of some of its fluid.

The following table gives approximately the proportions of the chief constituents of the bile :—

Water	85·0	per cent.
Bile salts	10·0	,,
Colouring matter and mucus	3·0	,,
Fats	1·0	,,
Cholesterin	0·3	,,
Inorganic salts	0·7	,,
	100·0	

Bile contains no structural elements nor any trace of albuminous bodies.

I. The bile acids are two compound acids, glyco-cholic and tauro-cholic, which exist in the bile in combination with sodium. The amount of each varies in different animals and at different times in the same animal. The bile of the dog and other carnivora contains only tauro-cholate of soda. In the ox the glyco-cholate of soda is greatly in excess. In man both are present, the proportion being variable, but the tauro-cholate is said to preponderate.

To separate these acids, bile is evaporated to one fourth its volume, rubbed to a paste with animal charcoal to remove the pigments, and carefully dried. The black cake is extracted with absolute alcohol, which dissolves the bile salts. From the strong alcoholic solution after partial evaporation the bile salts can be precipitated by ether. They first appear as an emulsion, and then form glistening crystals which are soluble in water or alcohol, but insoluble in ether.

From the solution of the two salts the glyco-cholic acid may be precipitated by neutral lead acetate, as lead glyco-cholate, from which the lead may be removed by sulphuretted hydrogen, and the acid precipitated from its alcoholic solution by the addition of water. The tauro-cholic acid may be obtained subsequently by treating with basic lead acetate.

Glyco-cholic acid when boiled with weak acids, alkalies, or baryta water, takes up an atom of water, and splits into cholic acid and glycin (amido-acetic acid). (See p. 43.)

Tauro-cholic acid, under similar treatment, splits into cholic acid and taurin (amido-ethyl-sulphonic acid). (See p. 43.)

Cholic acid occurs free in the intestines, the bile salts being split up in digestion and tauro-cholic and glyco-cholic acids separated.

The nitrogenous cholic acid is in a great measure eliminated with the fæces, while the taurin and glycin are re-absorbed into the blood with many of the other constituents of the bile, and are again probably utilised in the economy.

No traces of these bile acids can be detected in normal blood, and there is no accumulation of them in the body after the removal of the liver; hence it has been concluded that they are manufactured in the liver.

II. Mucus. The greater part of the mucus which the bile contains is produced in the gall bladder, and there added to the bile. Some mucus comes from the mucous glands in the bile-ducts, but unless the bile has remained in the gall-bladder there is but an insignificant amount of mucus present, as is seen when a fistula is made from the hepatic duct. The mucus passes in an unchanged state through the intestine, and is evacuated with the fæces.

III. The bile pigment of man and carnivora is chiefly the reddish form called *bilirubin*. It is insoluble in water but soluble in chloroform. It can be obtained in rhombic crystals, and is easily converted by oxidation into a green pigment, *biliverdin*, which is the principal colouring matter in the bile of many animals, and is not soluble in chloroform, but readily so in alcohol. Bilirubin is supposed to be identical with hæmatoidin, a deeply coloured material found by Virchow in old extravasations of blood within the body, and hence the bile pigment is said to be derived from the colouring matter of the blood. Probably the hæmoglobin of some red corpuscles which have been broken up in the spleen is converted into bile pigment by the liver.

Under the influence of decomposition bilirubin undergoes a change, taking up water and forming hydro-bilirubin; this occurs in the intestine, and the bilirubin is thus eliminated as the colouring matter of the fæces (stercobilin), which is probably identical with the urobilin of the urine.

IV. Fatty matters, the principal of which are lecithin (See p. 48), palmitin, stearin, olein, and their soda soaps.

V. Cholesterin ($C_{26}H_{44}O$) is an alcohol, and crystallises in clear rhombic plates, insoluble in water but held in solution by the presence of the bile salts. It can be obtained from gall-stones, the pale variety of which are almost entirely composed of it. The cholesterin leaves the intestine with the fæces.

VI. The inorganic salts are sodium and potassium chloride, calcium phosphate, some magnesia, and a considerable quantity of iron.

Tests for Bile.—The most important constituents of the bile, viz., the bile acids and pigment may be detected by appropriate tests, which are of great practical use :—

1. Pettenkofer's test for the bile acids :—To a fluid containing either or both bile acids add some cane sugar, and then slowly drop by drop, strong sulphuric acid. The solution turns to a cherry-red and then changes to a fine purple. As other substances, such as albuminous bodies, give under this treatment a similar colour in order to make the reaction a trustworthy test for bile salts, the two characteristic bands given by the spectroscope should also be observed.

   The following is said to be a more characteristic test :— Rinse out a porcelain capsule successively with the fluid to be tested, then with weak sulphuric acid, and finally with a weak solution of sugar, then heat to 70° C., when the capsule turns purple.

2. Gmelin's test for the bile pigments depends upon the fact that during the stages of oxidation the bilirubin undergoes a series of changes in colour which follow the sequence of the familiar solar spectrum. Place a few drops of the fluid to be tested on a white surface (a capsule or plate), and allow a drop of nitric acid, yellow with nitrous acid fumes, to run into it; as they mingle together the rainbow-like play of colour appears. This, when watched, will be found to consist of a series of changes to green, blue, violet, red, and yellow.

   The same can be observed by allowing the acid to trickle gently down the side of a test tube fixed in an inclined position so that it cannot be shaken, the play of colour can then be seen starting from the point of junction of the two fluids.

METHOD OF SECRETION OF BILE.

The secretion of the liver varies less in the amount formed in a given time than that of other digestive glands. Although the changes in the rate of its secretion are not so marked, they follow the same general rule as those of other glands, *i.e.*, after food is taken there is a sudden rise, then a gradual fall, followed by a second rise in the amount produced, as is so well seen in the case of the pancreas. Although hunger is said to check the secretion of bile, it is practically continuous as is the activity of all glands whose duty it is to eliminate noxious substances.

At the end of a period of fasting, the gall-bladder is always found greatly distended, because the secretion has continued to flow into that receptacle, and there has been no call for its discharge into the duodenum.

The amount of bile produced by dogs is much influenced by the diet. It is very great when meat alone is consumed, less with vegetable diet, and very small with a diet of pure fat. As a general rule the bile is more abundantly produced in herbivorous than in carnivorous animals.

The secretion of bile is also influenced by the amount of blood flowing through the organ. Ligature of the hepatic artery causes cessation of the secretion, and ultimately death, from malnutrition of the tissue of the liver.

These variations in the rate of secretion may depend on direct nervous influence, but no special secretory nerve mechanism has been discovered for the liver, and it is quite possible that the changes in the activity of the gland, which accompany the different periods of digestion may be accounted for by changes in the intestinal blood supply, which give rise to corresponding differences in the amount of blood flowing through the portal vein. If the vena porta be ligatured, an effect corresponding to the magnitude of the vessel is produced, the secretion is arrested and the animal dies; but it has been said that the secretion continues in the peripheral part of the lobules. If both the portal vein and the hepatic artery are ligatured the secretion at once stops.

The force with which the bile is secreted is very small. That is to say, the pressure in the ducts never exceeds that of the blood as occurs in the salivary glands; but, on the contrary, when a pressure of about 16mm. (·63 in.) mercury is attained, the evacuation of the bile ceases, and with a little increase of opposing force the fluid in the manometer retreats and finds its way into the blood. The low pressure which can be reached in the gall ducts does not imply any want of secretory power on the part of the liver cells, but merely that there exists a great facility of communication between the duct radicles and the blood vessels most probably through the medium of the lymphatics. This is made obvious by experiment, by which it can be shown that with a comparatively low pressure (200mm. = nearly 8 in. of water for a guinea-pig) any fluid can be forced into the circulation from the bile ducts.

It is observable also in the stoppage of the bile ducts in the human subject, when some at least of the bile constituents continue to be formed, and pass into the blood, where their presence is demonstrated by the yellow colour characteristic of jaundice. The ready evacuation of the bile is then a matter of great importance for health, the least check to its free exit causing the secretion, or as it might be equally well called excretion, to be forced into the circulating blood instead of into the gall passages. Under normal circumstances, the large receptacle of the gall-bladder being always ready to receive, the bile ensures its easy exit from the ducts, but the forces which cause its flow are extremely weak. The smooth muscle in the walls of the duct seem rather for the purpose of regulating than aiding the flow.

When food from the stomach begins to flow into the duodenum, the muscular coat of the gall-bladder contracts and sends a flow of bile into the intestine, which action is doubtless brought about by a reflex nerve impulse, for it is only when this part is stimulated that the bile flows freely from the bladder, and the acid gastric contents seem to be the most efficacious stimulus.

In the human subject the quantity of bile secreted has been found to be about 600 cc. (21 oz.) per diem in cases where there were biliary fistulæ. This would equal about 13 grms. per kilo of the body-weight.

In the guinea-pig and rabbit, it has been estimated to be about 150 grms. per kilo body-weight.

FUNCTIONS OF THE BILE.

1. *As Excrement.*—Although the great bulk of the bile is re-absorbed from the intestinal tract into the blood, and again used in the economy, some of its constituents pass off with the fæces, and are no doubt simply excrementitious matters that must be got rid of. Thus all the cholesterin, mucus, and colouring matter are normally eliminated, and a considerable quantity of the bile acids are split up, the cholic acid being found in the fæces.

2. *As a stimulant*, the bile is of considerable use, for it excites the muscles of the intestine to increased action, and thereby aids in absorption and promotes the forward movement of the food, and more particularly of those insoluble materials which have to be evacuated per anum: this stimulation may amount to mild purging.

3. *Moistening and lubricating.*—The bile adds to the ingesta an abundant supply of fluid and mucus, much of which passes along the intestine to moisten and lubricate the fæces and facilitate their evacuation. In cases of jaundice, or when the bile is removed by a fistula, the fæces are hard and friable, and with difficulty expelled, owing to the deficient fluid and mucus, as well as to the weaker peristaltic movements.

4. *As an Antiseptic*, the bile is said to have an important function to perform. Possibly it restricts the formation of certain of the bye products, such as the indol resulting from pancreatic digestion, but it is not *aseptic*, since bacteria abound and thrive in the intestine.

5. *Emulsification of fats.*—The bile has no doubt some power of forming an emulsion, but in a far less degree than the secretion of the pancreas; however, the mixed secretions are probably more efficacious than either separately, from the presence of the free fatty acids, which form soaps and aid in forming the emulsion.

6. *As an aid to absorption.*—The bile having some soap in solution has a close relationship to both watery and oily fluids, and possibly on

this account, as well as owing to a peculiar power possessed by the bile salts, a membrane saturated with bile allows an emulsion of fat to pass through it much more readily than if the same membrane were kept moistened with water. This can be seen experimentally with filter-paper.

7. *By neutralising acidity and precipitating peptones.*—When the acid contents of the stomach are poured into the duodenum and meet with a gush of alkaline bile—a copious cheesy precipitate is formed which clings to the wall of the intestine. This precipitate consists partly of acid albumin (parapeptone) and peptones thrown down by the strong solution of bile salts, and partly of bile acids, the salts of which have been decomposed by the hydrochloric acid of the gastric juice. With the bile acids the pepsin is mechanically carried down. Thus, immediately on their entrance into the duodenum the peptic digestion of the gastric contents is suddenly stopped not only by the precipitation of the soluble peptones and the shrinking of the swollen parapeptone, but also by the removal of the pepsin itself from the fluid and the neutralisation of the gastric fluid by the alkaine bile.

By thus checking the action of the gastric ferment the bile prepares the chyme for the action of the pancreatic juice.

CHAPTER XI.

FUNCTIONS OF THE INTESTINAL MUCOUS MEMBRANE.

In the Mucous Membrane of the intestine are found small glands of two distinct kinds. The glands of one kind, which are commonly called Brünner's glands, and are localised in the duodenum, are insignificant in number when compared with the others, Lieberkühn's

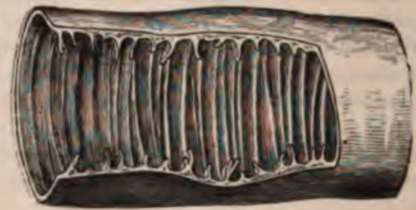


Fig. 76.—Portion of the Wall of the Small Intestine laid open to show the valvulæ conniventes. (Brinton.)

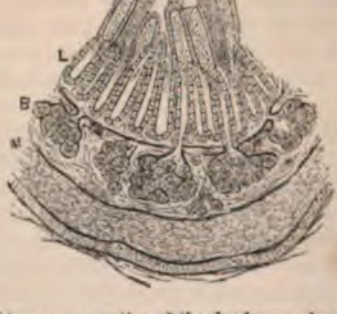


Fig. 77.—Drawing of transverse section of the duodenum showing Brünner's Glands (B) opening into Lieberkühn's follicles (L), (V) villi, (M) muscular coats.

glands, which are closely set and distributed over the entire intestinal tract in enormous numbers.

Brünner's glands form, in some animals, a dense layer in the submucous tissue of the beginning of the duodenum; they are small branched saccular glands resembling mucous glands in structure. Owing to their small size the secretion cannot be obtained in sufficient quantity to make satisfactory experiments in respect to its properties. It is said to dissolve albumin and to have a diastatic fermentative action, so that probably the secretion is analogous to that of the pancreas, as Brunner originally supposed. The quantity of fluid secreted by these glands is so small that its existence is not taken into account in speaking of the intestinal juice, by which is

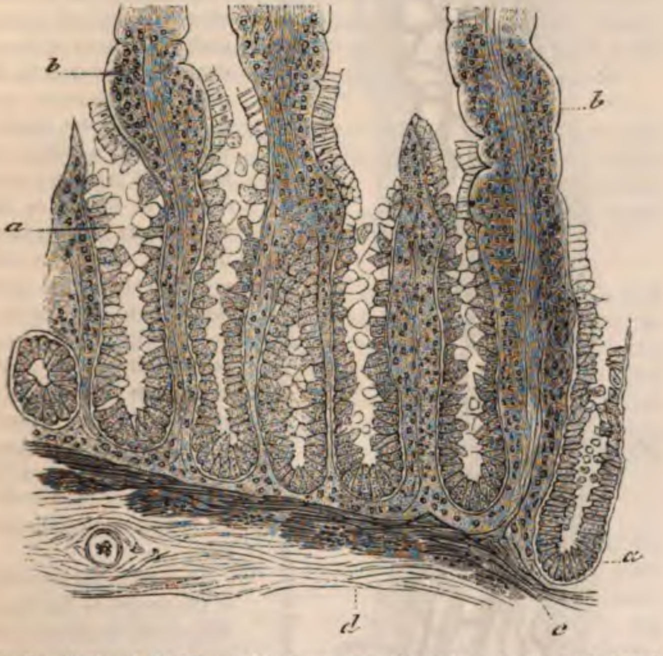


Fig. 78.—Section of the Mucous Membrane of small intestine, showing Lieberkühn's follicles (*a*) with their irregular epithelium and the villi (*b*) passing out of view; (*c*) Muscularis mucosæ; (*d*) Submucous tissue. (Cadiat.)

meant the fluid poured out by the innumerable short tubes or follicles of Lieberkühn.

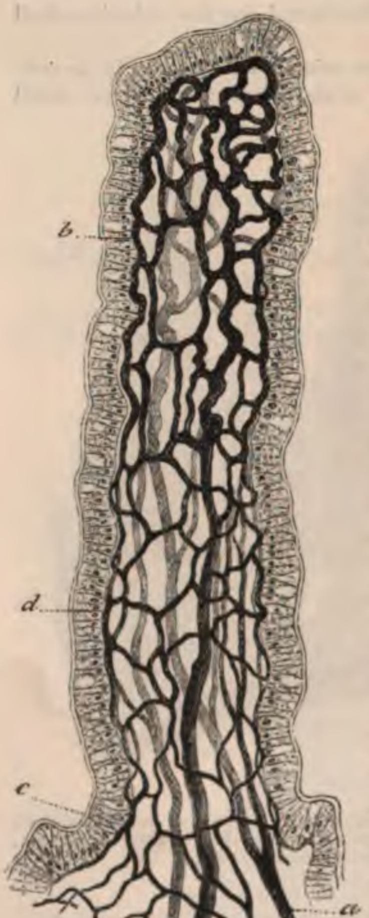


Fig. 79.—Villus with the capillaries injected showing their close relation to epithelium, some of the cells of which are distended with mucus. (Cadiat.)

These intestinal follicles belong to a very simple form of gland, each one being a single straight depression in the mucous membrane not deep enough to deserve the name of a tube. In the small intestine they are set as closely as the villi permit. In the large intestine, where the villi are absent, they are more closely set and are also deeper (Fig. 78). They are bounded by a thin basement membrane which is embraced by a close capillary network of blood vessels, and are lined by a single layer of cylindrical or spherical epithelial cells.

The epithelial covering of the processes known as villi which are studded all over the mucous membrane of the small intestine produce some mucus.

Method of Obtaining Intestinal Secretion.—Considerable difficulty has been found in obtaining the proper intestinal juice free from admixture with the secretions of the liver and pancreas which are carried along and mixed with it. A short portion of the small intestine has, however, been successfully isolated from the rest without injuring the mesentery or its blood-vessels. One of the extremities of the isolated portion was closed, and the other was retained by sutures at an opening in the abdominal wall. The cut ends of the remainder of the intestine were at the same time united, so that the continuity of the alimentary tract was preserved. Thus, a limited piece of gut formed a cul-de-sac from which the fluid could be collected through a fistulous opening.

Characters of the Secretion.—The fluid obtained from such a fistula is a thin opalescent yellowish fluid with a strong alkaline reaction and a specific gravity of 1011. It contains some proteid and other organic material, a ferment and inorganic salts in which sodium carbonate preponderates.

Mode of Secretion.—The secretion flows but slowly from such a fistula but the amount increases during digestion, showing that the secretion of the intestine is under the control of some nerve centre which can call the entire tract into action when one part is stimulated. Moreover, the local stimulation of the mucous membrane makes it red, and causes it to pour out a more abundant secretion. Beyond this little is known of the nervous mechanism or the local cell-changes which accompany the formation of the secretion.

Functions of the Intestinal Juice.—All the properties of the secretion of the pancreas have been accorded to the intestinal juice. It is said to have a ferment, capable of being extracted with glycerine, which can convert cane sugar and starch into grape sugar, and bring about lactic fermentation. It dissolves fibrin very slowly and still less easily other proteids. It is also said to emulsify fats. However, the observations as to its digestive properties are very discordant, experiments giving opposite results in different animals, and in the hands of different persons even in the same animal. From the foregoing account of the intestinal secretions it may be seen that the changes which the various kinds of food undergo on their way through this part of the alimentary tract are numerous; a short review may therefore be useful:

When the acid gastric chyme flows into the duodenum a flow of bile takes place from the gall-bladder and at the same time the secretions of the pancreas, Brünner's glands, and Lieberkühn's follicles are poured copiously into the intestine. The bile meeting with the turbid fluid chyme causes it to change to a soft cheesy granular mass, the appearance of which depends chiefly on the precipitation and shrinking of the parapeptone and peptones. The pepsin is rendered powerless, both it and the bile salts being carried down with the precipitate. Gastric digestion is thus arrested and the onward flow of the fluid chyme checked. As the alkaline pancreatic and intestinal juices meet this semi-fluid cheesy mass the conversion of starch into sugar proceeds rapidly, even the raw starch granules being thus changed. The small oil globules come in contact with the alkaline mixture of bile and pancreatic juice. The pancreatic secretion splits up some of the fat separating the fatty acid from the glycerine radicle. Some of the soda of the bile salt is substituted for the latter, and uniting with the fatty acid forms a soap. In such a mixture as this—an alkaline fluid with proteid and soap in solution—a fine emulsion is readily formed, as can be seen by adding sodium carbonate to some rancid oil. The free acid (the cause of rancidity in the oil) unites with some soda to form a soap which in the alkaline mixture enables the oil to be converted into an emulsion by even slight agitation, so that the pancreas, by setting free fatty acid, and the bile possibly by contributing some soda, aid one another in giving rise to a definite but small amount of soap.

The precipitated parapeptone and peptone and the finely divided proteid are presented to the pancreatic juice in a form which it can most easily attack, and thus the conversion of proteid into peptones goes on rapidly.

How far the peculiar action of trypsin on proteids, converting them further into leucin and tyrosin, goes on in normal digestion is not known, but it is probable that the production of these bodies is increased with the over-abundant ingestion of proteid or a purely meat diet, and is then useful as a means of preventing the injurious effects of too great proteid absorption.

The gastric chyme is therefore completely changed in the duodenum, and in the other parts of the small intestines we find in its stead a thin creamy fluid which clings to the mucous membrane coats over its folds (valvulæ conniventes) and surrounds the long villi of the jejunum, &c. This intestinal chyme is the form in which the food is presented to the mucous membrane for absorption. It resembles somewhat by its whiteness the fluid called chyle which flows in the lacteals, and formerly was considered to be identical with it. This creamy lining is the chief material found in the upper part of the small intestine, the coarser parts of the food being hurried on by peristaltic action to the large intestine.

In the large intestine the secretion of the long closely-set Lieberkühn's follicles is the only one of importance. Its reaction and that of the mucous membrane is alkaline, but the contents of the colon is acid owing to certain fermentative changes which go on in this part of the intestine.

Of the changes brought about in the large intestine by the agency of the digestive juices we know but little. Judging from the large size of the cœcum and colon in herbivorous animals, we are prompted to conclude that vegetable substances, possibly cellulose, may be dissolved here, but we do not know how this is accomplished. Although devoid of villi, the large intestine can certainly absorb readily such materials as are in solution. As the insoluble materials pass along the small intestines the supply of fluid is kept up to about the same standard, the absorption and secretion being about equal; but in the large intestine, the absorption of the fluid so exceeds the secretion in amount that the undigested materials are gradually deprived of their fluid, and are converted into soft solid masses which pass on to be added to the fæces.

Owing to its absorbent power the large intestine is a ready and rapid channel by which materials can be introduced into the system in cases in which the stomach is too irritable to retain food.

The quantity of fæces evacuated in the day depends upon the kind of diet, being greater with a vegetable than meat diet, averaging about 150 grammes a day (60–250 grms.). This amount may be greatly increased by largely partaking of indigestible forms of food. The more rapid the passage of the ingesta through the intestine the greater is the amount of fluid remaining with the fæces, so that any stimulant to the intestinal movements reduces the consistence of the fæces and facilitates the evacuation. The fætor depends in a great measure on the presence of indol, which is an outcome of pancreatic digestion, and also upon the presence of certain volatile fatty acids. The colour depends upon the amount of the bile pigment and the degree of change the latter has undergone.

The fæces are composed of (1) the undigested parts of the food, and (2) the useless or injurious parts of the secretions of the various glands. In the first category we find perfectly indigestible stuffs such as yellow elastic tissue, horny structure, portions of hairs from animal food, and cellulose woody fibre and spiral vessels from plants, and also masses of digestible substances which have been swallowed in too large pieces to be thoroughly acted on by the secretions. All forms of food may thus appear in the fæces, but most commonly vegetable substances are conspicuous.

In the second category we find a variable quantity of mucus and the decomposed colouring matter of the bile, together with some cholic acid, cholesterin, &c.

A few inorganic substances are found, mainly those which diffuse with difficulty, as calcium salts and ammonio-magnesium phosphate.

PUTREFACTIVE FERMENTATIONS IN THE INTESTINE.—With the air and saliva which are swallowed mixed with the food, large numbers of the lower organisms existing in them are introduced into the alimentary canal.

The effect of these organisms is to produce certain fermentative changes quite distinct from the action of the special ferments peculiar to the digestive fluids.

This is proved by the composition of the gases found in the intestine. Atmospheric air only is introduced from without, and this is not found in any part of the alimentary tract, the oxygen soon being absorbed and the nitrogen left, while a quantity of carbonic anhydride and hydrogen from the fermentation of the sugar are set free, lactic and butyric acids being produced at the same time.

Indol and skatol are also formed by putrefactive fermentation of the leucin and tyrosin, although this is in a great measure held in check by the antiseptic nature of the bile.

It is in the large intestine that putrefactive fermentations have the greatest effect, the acid reaction being caused by the various acids produced.

With regard to the interesting question,—Why do not the digestive fluids dissolve the tissues of the organs in which they are contained, we cannot speak positively. We cannot now say that the "vital principle" has a protective influence, for we know the fact that a tissue being alive is not sufficient to ward off the digestive action of the alimentary juices, since the limb of a living frog is digested when introduced through a fistula into the stomach of a dog; and when the intestinal juice trickles from a fistula the neighbouring skin, the snout, and the tongue of the animal soon become eaten away owing to its licking the fluid, which rapidly digests these parts so as to destroy the skin and even expose the blood vessels.

We can however modify John Hunter's statement that the resisting power was associated with the life of the structures, by saying that it is not the property of an abstract "vital principle," but a special resisting power dependent upon the specific character of the vital processes of certain textures.

CHAPTER XII.

ABSORPTION.

In order that the food-stuffs when altered by the various processes described under digestion, may be of any real use to the economy, the nutritive materials must be distributed through the textures and organs. For this purpose they must pass through the lining membrane of the alimentary canal, and obtain admission to the blood, which is the common mode of intercommunication between the various parts of the body.

The nutrient part of the food has then to be *absorbed* out of the alimentary canal by the surrounding tissues, and mixed with the general circulating fluid.

But the blood is separated from the intestinal contents by a barrier, which for it at least is impassable, although it exerts considerable pressure, and therefore tends to burst out from the vessels.

The question then arises—How does the elaborated chyme make its way through this barrier, which is sufficient to prevent the flow of blood into the intestinal tract?

The general answer is easily given, viz. :—the blood cannot pass through an animal membrane. But this is not a satisfactory solution of the question, for sometimes, under certain circumstances, the blood does pass through the wall of the vessels, and normally the plasma escapes from the capillaries into the tissues, in order to nourish them. We must further remember, in considering this point, that the wall of the vessels and the membrane lining of the intestine are both made up of living cells which are endowed with a capability, co-incident with their lives, of controlling any passage through or between them. Some of these cell-guards, which we might call secreting agents, do allow, or rather cause a passage of fluid from the blood to the intestinal cavity, and, as we shall presently see, others of them induce a passage of the nutritious materials from the intestinal canal into the surrounding tissues.

In order clearly to understand the method by which absorption is accomplished, it is necessary to have some idea of the absorbent system generally; it may be well, therefore, at this place to give a brief account of the construction of the special apparatus which

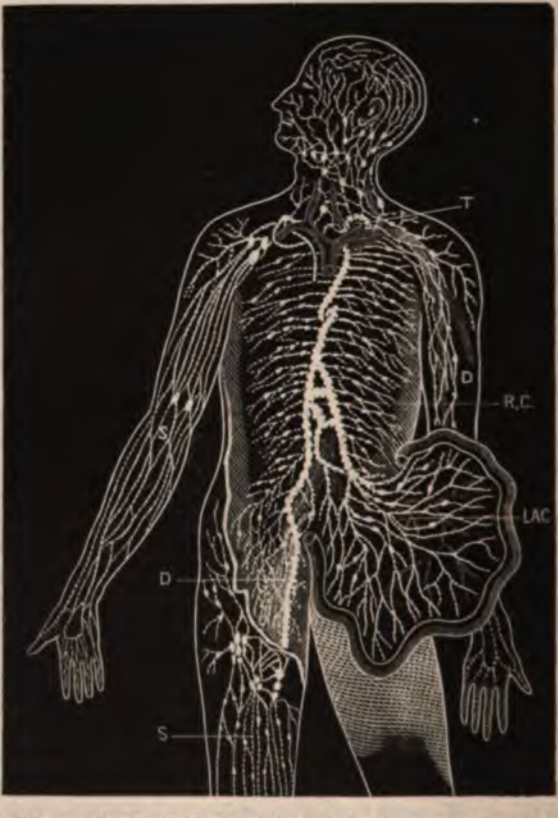


Fig. 80.—Diagram showing the Course of the Main Trunks of the Absorbent System. The lymphatics of lower extremities, &c., meeting the lacteals of intestines at the receptaculum chyli (R. C.), which opens into the thoracic duct. The superficial vessels are shown in the diagram on the left arm and leg (S.), and the deeper ones on the arm to the right (D.). The glands are here and there shown in groups. The small right duct opens into the veins on the right side. The thoracic duct discharges into the union of the great veins of the left side of the neck (T.).

carries on this function. Although the absorbent vessels form one continuous system, they may be conveniently divided into two provinces, namely, interstitial and surface absorption. A certain modification of the latter, called the lacteal system, occurs in the alimentary canal, and is described under intestinal absorption.

I. *Interstitial Absorption.*

The blood flowing through the body in delicate capillary vessels yields to the various tissues a kind of irrigation stream of plasma, which, leaving the capillaries, permeates their substance so that every texture is saturated with nutrient fluid. The surplus of this irrigation stream is collected and carried back to the blood current by a special set of fine vessels with slender walls, called the lymph vascular system, which act as drains to the tissues, and pour their contents into the veins.

When the nutrient fluid escapes from the capillaries, it lies in the interstices in the tissue elements, and here bathes the tissue cells which commonly occupy these interstices. (Figs. 81 and 86.)

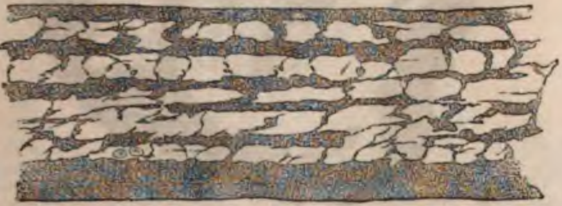


Fig. 81.—Tendon of Mouse's Tail treated with nitrate of silver, showing clefts or cell-spaces around the bundles of fibrils as white patches. These interstices may be called the smallest lymph-channels or spaces. (Schäfer.)

Communicating freely with the interstices of the tissues are irregular anastomosing flattened channels, which convey the lymph or any fluid forced between the tissues into vessels with more definite walls. These vessels, which are lined with characteristic endothelium, form a more or less dense network of lymphatic capillaries, from which spring the tributaries of the lymph vessels. (Figs. 82 and 83.)

The lymphatic vessels are throughout slender thin-walled channels with close-set valves, usually in pairs, and with frequent anastomoses. They lie embedded in the connective tissue, and when empty, are difficult to see, owing to their extreme delicacy. They converge towards a central vessel called the thoracic duct, which, passing from the abdominal cavity, through the thorax, reaches the left side of the neck, and opens into the angle of junction of the two great veins from the head and upper extremity. (Fig. 80.) On the right side a smaller trunk conveying the lymph from the right arm and that side of the head, chest, and neck, opens into the corresponding venous trunks.

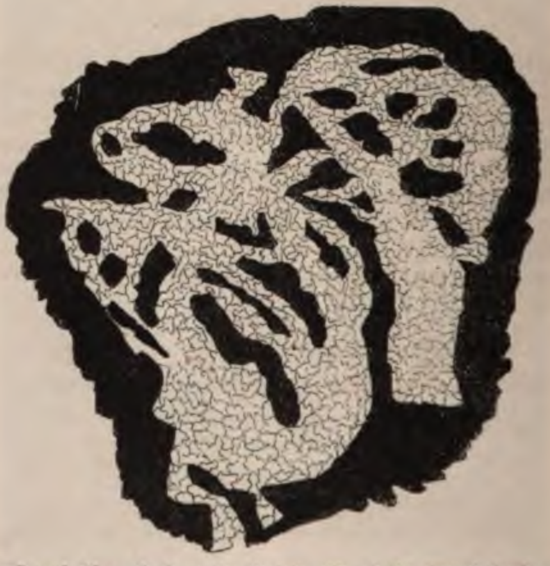


Fig. 82.—Lymph Channels from the thoracic side of the central tendon of the diaphragm of the rabbit, treated with silver nitrate. The fine lines indicate the boundaries of the endothelium cells lining the lymph channels. The dark part shows the islets between the lymphatic network. (Klein.)

The thoracic duct is much larger than any of the numerous tributaries which enter it at close intervals from all directions.

Its lower extremity or point of origin is an irregular dilatation called the *receptaculum chyli*, because the lymphatic vessels from the stomach and intestines, or lacteals as they are called, pour their contents into it. The chyle from the intestines thus flows into the same main channel as the lymph which is derived from the drainage of the tissues and organs of the lower extremity, the trunk and left side of the head and neck and arm; and the two fluids are mixed in the receptaculum chyli, and the other parts of the thoracic duct.

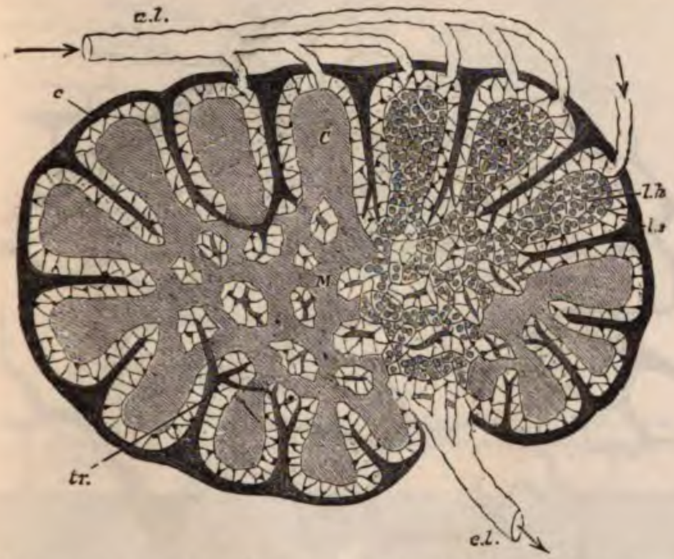


Fig. 83.—Diagram of a Lymphatic Gland, showing (*a l*) afferent and (*e l*) efferent lymphatic vessels; (C) Cortical substance; (M) Medullary substance; (*c*) Fibrous coat sending trabeculæ (*t r*) into the substance of the gland, where they branch, and in the medullary part form a reticulum, the trabeculæ are surrounded by the lymph path or sinus, which separates them from the adenoid tissue (*l h*). (Sharpey.)

Along the course of the lymphatic vessels are numerous small bodies called lymphatic glands or follicles, which are composed of masses of a delicate trellis-work of adenoid tissue, packed with nucleated protoplasmic cells, called lymph corpuscles, the combination making what is known as lymphoid tissue. (Fig. 84 (*lh*) and 85). These masses of cells and their delicate supporting reticulum are enclosed in a fibrous case or capsule from which branching trabeculæ pass into the gland and separate the masses of lymphoid tissue from one another. Through the convex side of the capsule the lymph channels enter and pour their contents. The lymph then flows through irregular paths, which lie between the lymph follicles next to the capsule and trabeculæ, and lead to the concavity of the gland from which the efferent vessel escapes.

These lymph glands occur in groups in the flexures of the limbs, the recesses of the neck, and the thoracic and abdominal cavities, a large number being placed in the mesentery, in the course of the intestinal lacteals.

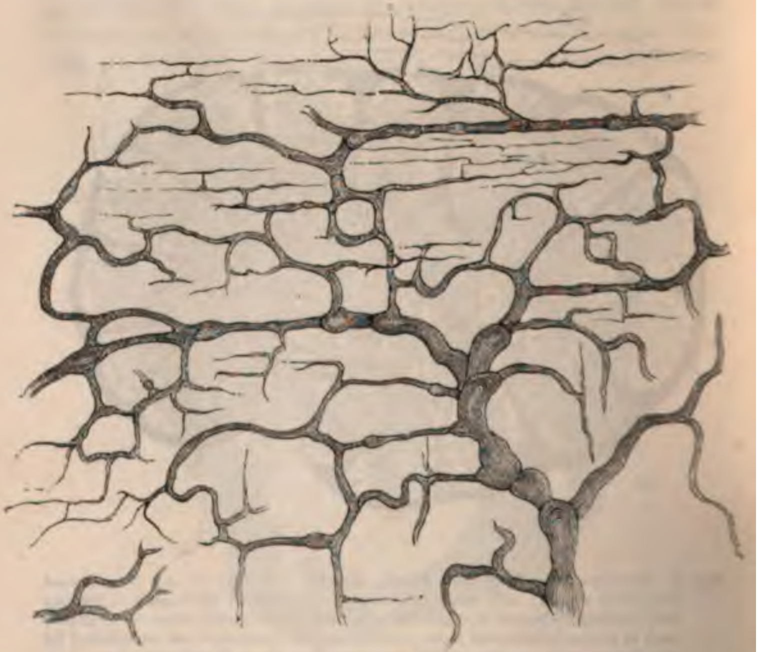


Fig. 84.—Lymphatic Network from between the Muscle Coats of the Intestinal Wall, with fine vessels and many valves, causing the walls to bulge. (Cadiat.)

In the submucous tissue of the intestine there is much of this lymphoid tissue, arranged in numerous small follicles, which doubtless have a similar function to the lymph glands found elsewhere.

There are various modes of origin of the lymphatic vessels which are more or less characteristic of the different parts in which they occur.

In the connective and allied tissues there are variously formed fissures or splits, which can be filled with fluid forced into the tissues by puncturing the skin with the nozzle of a fine syringe, such as is used for hypo-dermic injection.

These fissures contain the protoplasmic units of the tissue, and

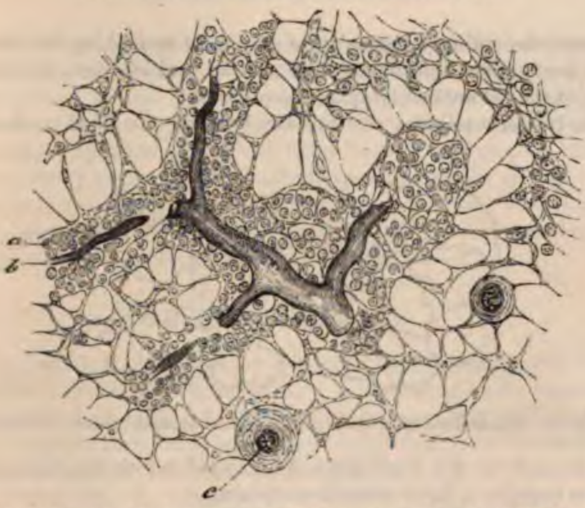


Fig. 85.—Section through the central or medullary part of a Lymphatic Gland, showing adenoid tissue (*a*) containing capillaries (*b*) and a fibrous trabecula (*c*) containing an artery. (Cadiat.)

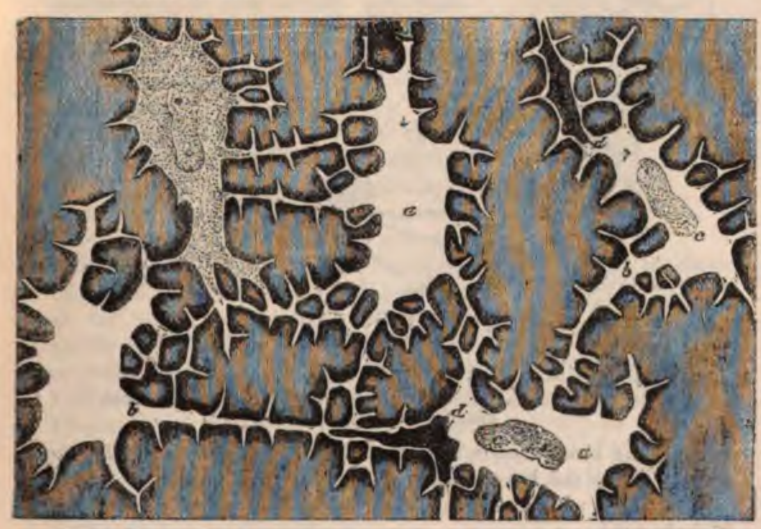


Fig. 86.—Clefts in the Corneal Tissue of a Frog treated with nitrate of silver, which leaves the spaces clear and stains the intermediate structure. These clefts (*a*) and their processes (*b*) form the lymph canalicular system, and at the same time are the spaces in which the corneal corpuscles reside. (Klein.)

transmit the ordinary transudation stream for nourishing the tissues. They freely communicate one with another, and lead into the beginnings of the network of lymphatic capillaries.

The lymph capillaries run midway between the blood capillaries, and are made up of a single layer of nucleated endothelial cells, which can be brought to light with silver staining.

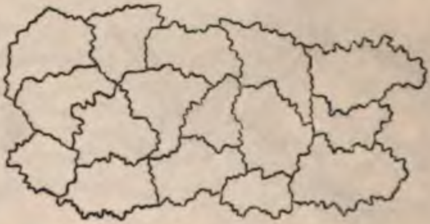


Fig. 87.—Endothelium from serous surface without stomata (nitrate of silver).

In some tissues, such as that of the central nervous system, the liver and bone, the lymph vessels commence as channels encircling the blood vessels, or perivascular lymph spaces, as they are called. Here the lymph channels form a kind of sheath for the minute blood vessels, and pass along to the connective tissue forming the adventitia.

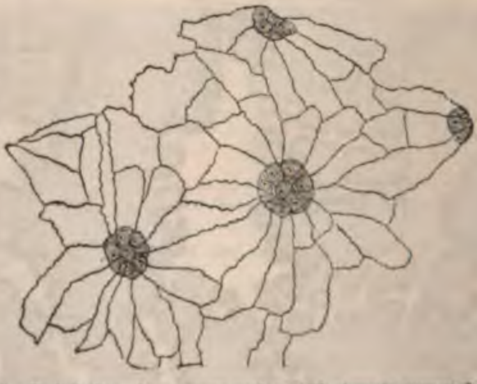


Fig. 88.—Endothelium from serous surface with stomata surrounded with granular protoplasmic cells.

The lymph vessels may also be said to commence on the surface of serous membranes which are intimately connected with the lymphatic system, and may indeed be regarded as nothing more than exaggerated lymph spaces. In most parts of the endothelial surface of serous cavities are a number of so-called stomata, or small apertures surrounded by a few cells, which differ from the ordinary endothelial cells in every respect, and probably have to control the passage of the fluid from the serous cavity into the lymph vessels. These *stomata* may be regarded as the commencement of the dense network of lymph capillaries, which lie in the subserous tissue.

II. *Intestinal Absorption.*

The intestinal absorbents are merely a special department of the lymphatic system, which, on account of the white chyle they carry being seen through their transparent walls, have been called lacteals, their function being to take up the nutrient fluid from the intestinal cavity, as well as to drain the tissue in which they lie. In order to fulfil their function, they are arranged in a particular way, especially adapted to the peculiar construction of the mucous membrane lining this part of the alimentary tract, which must be briefly described before the mechanism of absorption can be understood.

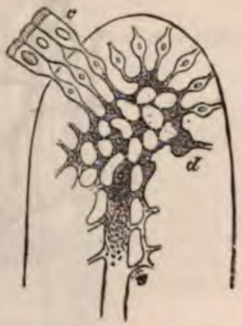


Fig. 89.—Diagram of relation of the epithelium to the lacteal radical in villus. The protoplasmic epithelial cells supposed to be connected to the absorbent vessel by adenoid tissue. (after Funke).

The most striking characteristic of the lining membrane of the small intestine is the existence of *villi*, which are only found in this part of the alimentary tract. They consist of nipple-shaped processes projecting into the intestinal cavity so closely set that they have the appearance of the pile of velvet; and being just visible to the naked eye, they give the mucous membrane, when washed and held under water, a peculiar velvety look. On account of these villi, and also of the ring-like folds of mucous membrane in the upper part of the small intestine, the extent of surface over which the chyme has to travel is greatly increased.

The surface of the villi is covered over with a simple layer of columnar epithelial cells in continuity with the epithelium lining the rest of the intestinal tract. The free surface of these cells is marked by a clear margin which is composed of a row of minute rods closely packed together, while the deep-seated end of the cells is branched, and appears to be prolonged into the substance of the villus and in some way to be connected with the supporting retiform tissue. Some of the cells are seen to swell upon the addition of certain re-agents, owing to their containing mucus, which gives them a peculiar goblet shape; hence they are called goblet cells. These cells occur at intervals, and some observers consider that they form a distinct variety of cells, differing from the neighbouring cells just as the border cells of the stomach-glands differ from the central cells.

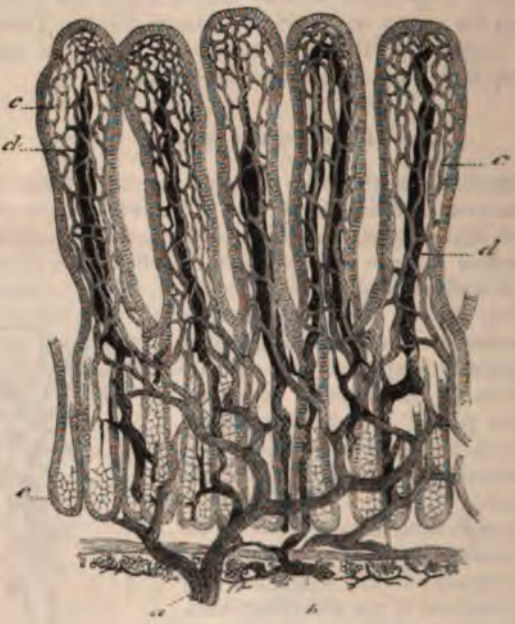


Fig. 90.—Section of Intestine of a Dog in which the blood vessels (*c*) and the lacteals (*d*) have been injected. The blind ending or simple loop of the black lacteal is seen to be surrounded by the capillary network of the blood-vessels. (Cadiat.)

The body of the villus is composed of a very delicate kind of

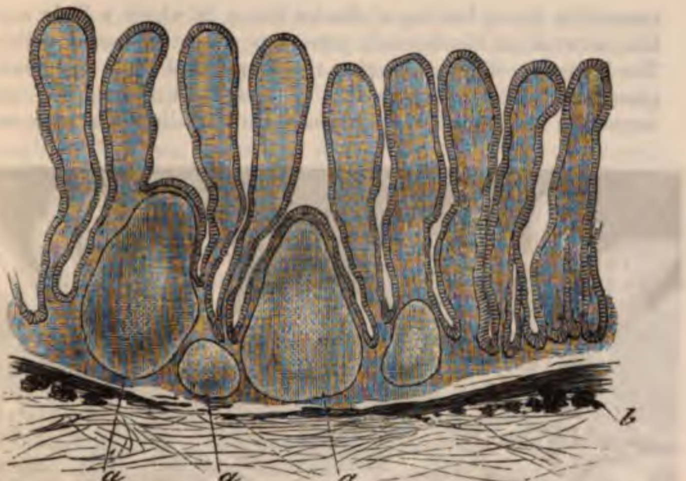


Fig. 91.—Diagram of Section of the Mucous Membrane of the Intestine, showing the position of the lymph follicles (*a*). (Cadiat.)

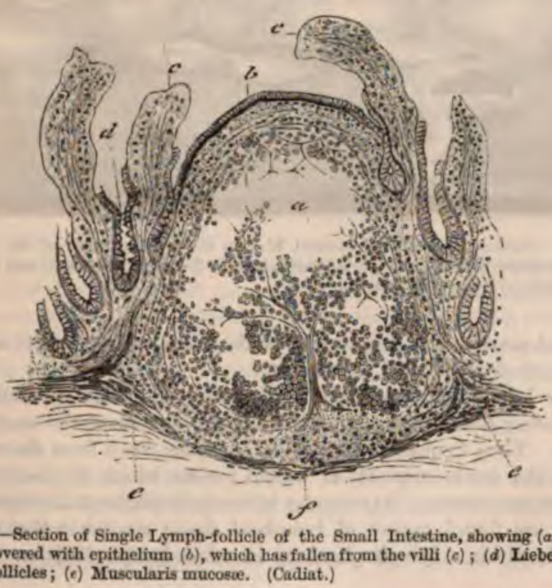


Fig. 92.—Section of Single Lymph-follicle of the Small Intestine, showing (*a*) follicle covered with epithelium (*b*), which has fallen from the villi (*c*); (*d*) **Lieberkühn's follicles**; (*e*) Muscularis mucosæ. (Cadiat.)

connective tissue, forming a slender frame in which a little cage-like network of blood-vessels surrounds a central lacteal radicle. The interstices of this connective tissue are filled with pale protoplasmic cells, like those formed in the lymph. Under the basement membrane forming the foundation of the epithelium are some unstriated muscle cells which embrace the villus and are able to squeeze it and empty the vessel it contains.

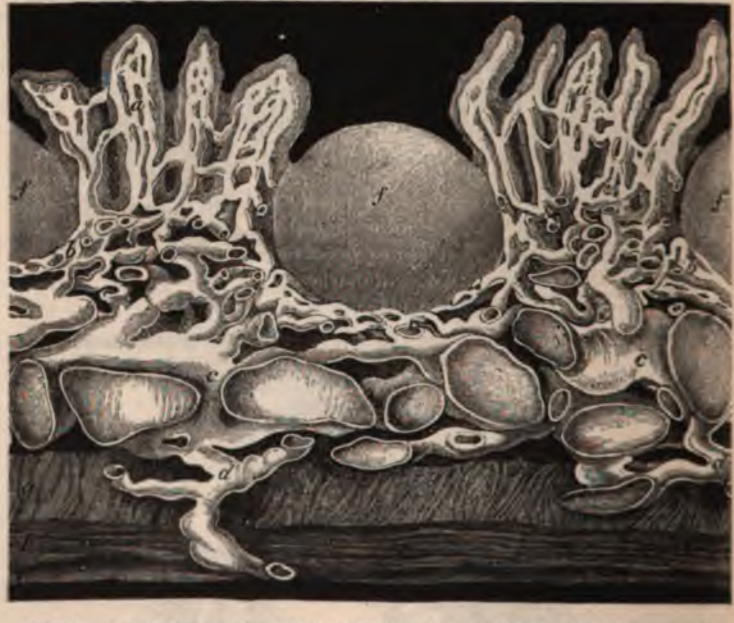


Fig. 93.—Section through the Intestinal Wall in the neighbourhood of the grouped lymph-follicles (*f*) (Peyer's patch), showing the upper narrow (*b*) and the deep wide (*c*) lymphatic plexuses.

The lacteal radicles which lie in the villi are sometimes double, and have a communication with the lymph spaces of the connective tissue. They frequently branch as they pass down from the villi to reach the dense network of lacteal vessels which lies beneath the mucous membrane. At irregular intervals throughout the submucous tissue are found masses of lymphoid tissue similar to that seen in packets within a lymph gland or in other lymph follicles. These are either isolated (solitary glands) or collected into groups (agminated or Peyer's glands). Though called glands by anatomists, it should be borne in mind that they are in no way connected with the secretion of any of the intestinal juices, but belong to the absorbing arrangements of the intestine. Around these solitary and grouped lymph follicles are spaces and networks from which the lacteal vessels arise (fig. 93).

MECHANISM OF ABSORPTION.

Formerly absorption was supposed to take place by means of the blood-vessels alone, but after the discovery of lymph and chyle vessels by Caspar Asellius the belief in the direct absorption by the blood-vessels was completely abandoned, and all the work of absorption was attributed to the lymphatics. However, ample evidence exists to show that substances capable of absorption can make their way into the blood-vessels of any part not protected by an impermeable covering like the horny layer of the skin, and thus be carried directly to the general circulation. The share taken by the blood-vessels in interstitial absorption in the tissues is not defined, and when no impediment to the lymph-flow exists is probably very small.

In the absorption from the alimentary tract, however, the blood-vessels appear to take a considerable part.

How far the tissue interspaces and the local lymph-channels, many of which surround the blood-vessels, aid in the passage of substances into the blood currents is not known; but most likely they have some such effect, for the experiments showing direct absorption by the blood-vessels leave the local lymph-channels in operation, while at the same time the normal flow of lymph towards the thoracic duct is more or less prevented.

Any part which has only the protection of a single layer of epithelial cells well supplied with superficial blood-vessels has also a supply of absorbent vessels, and therefore is capable of absorbing materials in solution which are in contact with the surface, and large quantities of fluids and solutions of various materials are absorbed from the stomach and large intestine—partly, no doubt, by means of the lacteals or lymphatics, and partly by the minute blood-vessels themselves.

However, the small intestine seems to be the part of the alimentary tract which is especially adapted for taking up the materials elaborated from the food.

In the upper part of the small intestine the valvulæ conniventes are most marked, and the villi are long and closely set together. It is here we find the thickest layer of creamy chyme covering the mucous membrane, but seldom any masses of partially digested food. All these points, which are directly related to absorption, tend to show that the upper part of the intestine is the part specially adapted for this purpose. The chyme which clings to the mucous membrane contains all the substances which are destined to pass into the economy. Into this mixture the villi dip, so that each villus is completely bathed with chyme. From what has been said of the construction of the villi it is obvious that such an arrangement is admirably well adapted to the absorption of the nutrient material, which has every facility for making its way into the lacteals and blood-vessels.

The principal ingredients in the chyme may now be examined in detail with reference to their powers of being absorbed.

Water can be absorbed from the intestinal tract in almost unlimited quantity, but not so with solutions of salts. The amount of the solution of any salt capable of absorption seems to depend on its endosmotic equivalent. The lower the endosmotic equivalent the more readily the solution passes into the blood-vessels. In those cases where the equivalent is very high, such as magnesium sulphate, there is a tendency of the fluid to pass out from the blood-vessels into the intestinal cavity; hence the watery stools caused by this and such-like saline purgatives.

Among the carbo-hydrates we need only take into account the sugars, for starch unchanged is but little if at all absorbed. Only a certain quantity of sugar can be taken up by the intestinal absorbents, since some is found in the fæces when the amount taken with the food exceeds a certain quantity. Some of the sugar in the intestine moreover undergoes fermentation, by which it is converted into lactic and butyric acid. How much of the sugar is absorbed as lactic and butyric acid has not been determined, but the amount of sugar found in the portal vessels or lacteals does not at all correspond with the amount that disappears from the cavity of the intestine.

Ordinary proteids, being colloids, can only pass slowly through an animal membrane, hence they are said to be changed into peptones under ordinary circumstances before they are absorbed. Their absorption takes place chiefly in the stomach, and is completed in the small intestine, as only a small quantity of albuminous substances is found in the large intestine even after an excessive meat diet. The more concentrated the solutions of peptones are the more rapidly are they absorbed, and the rate of absorption is greatest at first and then by degrees diminishes. The presence of alkali is also said to facilitate the absorption of peptones. It is a curious fact that neither in the lacteals nor in the portal blood can any quantity of peptone be found, even during active proteid digestion; so that it is impossible to trace out their course as peptones, or to say by which set of channels they reach the blood. If we assume that all proteids must be absorbed as diffusible peptone, we are forced to conclude that during their passage from the intestinal cavity they must be reconverted into ordinary proteids. But we know that soluble forms of albumin are to some extent diffusible (when a solution of salt is used) through a dead animal membrane. But even were this quite impossible it would not preclude the possibility of their passing through the intestinal wall, which presents no such obstacle, for it is a living structure that can overcome such physical difficulties as the non-diffusion of colloids. When we know that solid particles of fat can enter the lacteals we can have no difficulty in believing that a solution of albumin is admitted. We may then conclude that it is not only possible, but even probable, that a good deal of proteid is absorbed as ordinary soluble albumin. A certain limit to proteid absorption exists, so that any albuminous materials above the maximum that escape conversion into leucin and tyrosin are thrown off with the fæces.

In the absorption of water, watery solutions of salts, sugars, and peptones, there are no physical difficulties to be got over; so that we are in the habit of speaking confidently about the mechanism of their absorption, although in all probability many circumstances of which we are ignorant co-operate in bringing about the results which seem to us so simple.

It is not the same, however, with the fatty food-stuffs. A small quantity of these may no doubt be split up into soluble glycerine and fatty acids, which are at once changed into soluble soaps, and in this condition are capable of simple osmotic transmission into the blood-vessels or lacteals. However, the greater portion of the fat enters the lacteals as such in a condition of a fine emulsion, *i.e.*, composed of solid particles. This process is difficult to reconcile with our physical experiences; for, however finely divided it may be, fat emulsified does not pass through an animal membrane more freely than ordinary fluid fat. The fat emulsion is chiefly taken up by the villi of the small intestines, as in the stomach it exists only in large fluid masses or globules, and the amount of fat found in the large intestine is small, unless used as food in great excess. This can also be seen in examining the absorbent vessels after a fatty meal when those which carry materials from the stomach and large intestine are clear and transparent, while those coming from the small intestines are filled with the white milky fluid which gives them their special name of lacteals. There is a limit to the absorbent capacity of the intestine for fatty matters, for when a great excess of fat is eaten it appears with the excrement, sometimes giving rise to adipose diarrhœa, thus showing that the amount has exceeded this limit.

The important question remains, how does the fat emulsion make its way through the intestinal mucous membrane? That it really does so there can be no shadow of doubt; for it disappears from the intestinal cavity, and can be detected in the chyle with the aid of the microscope more easily than any other of the intestinal contents that are absorbed.

It has been shown that while a membrane moistened with water acts as a complete barrier to a fat emulsion, and only after prolonged exposure under high pressure allows traces of fats to pass, the same membrane when saturated with bile will without pressure permit the passage of a considerable amount of oil. It has therefore been suggested that the epithelial cells of the mucous membrane are more or less moistened with bile, and the particles of fat in the emulsion are also coated with a film of bile or soap. Thus they are enabled to pass into the epithelial cells, in which they can be detected during digestion. The bile or soapy coating of the fat particles may no doubt aid in their transit through the various obstacles on their way to the lacteal radicles. But the course taken by the fat particles can hardly be explained in this way, and many circumstances force us to the belief that the activity of the protoplasm of the epithelial or of some special wandering cells is the real factor in the case. When the fat is once scattered through the protoplasm of the cells and their prolongation into the delicate connective tissue of the villi, then in all probability other forces, such as the contraction of the villi, may aid in their further movement to the central lacteal space of the villus.

The exact utility of the marginal bands of rods or pores which characterize the surface of the intestinal epithelium is not known, though it is supposed to be connected with the absorption of fats.

We may conclude then that the passage through the intestinal wall of some of the materials taken as food may possibly be accomplished by mere physical processes, but it is probable that the vital activity of the epithelial cells modifies or controls their absorption. The passage of the fat can only be explained by the aid of the direct activity of cells which by amœboid movement take up the fine particles and pass them on to the interstices of the connective tissue of the villi.

Lymph and Chyle.

As these two fluids are mixed together in the thoracic duct, whence the lymph is commonly obtained for examination, they had better be considered at the same time.

As we should expect, the fluids coming from the tissue drainage, from the lymphatic glands, and from the lacteals of the alimentary tract form an opaque mixture which holds a considerable quantity of proteid in solution, and contains a number of morphological elements, viz.: (1), protoplasmic cells similar to those found in the lymph follicles, and in most essential points identical with the pale cells found in the blood; (2), some red-blood corpuscles which give the fluid in the thoracic duct a pinkish colour; (3), a quantity of very finely divided fat, which varies in proportion to the amount of fat recently digested; (4), other minute particles of unknown function and origin.

When removed from the body and allowed to stand, the lymph becomes converted into a soft jelly. This coagulation no doubt depends upon the chemical changes in the lymph which give rise to fibrin. This subject will be discussed more fully in a future chapter. The amount of fibrin formed in the lymph is very small, and therefore the clot is very soft, and shrinks considerably. The quantity of chyle which can be obtained from the lacteals is also small, and therefore the thorough investigation of it is difficult. The fluid from the tissues differs from the mixed lymph in appearance and constitution only during digestion, and then chiefly in containing a greater amount of fat and solids derived from the intestinal cavity. The lymph of the thoracic duct contains three forms of proteid: (1), serum albumin, which can be coagulated by heat; (2), alkali albumin precipitated by neutralization; and (3), globulin. It also contains in solution soap, cholesterin, grape-sugar, urea, leucin, and some salts, particularly sodium chloride, and the sulphates and phosphates of the alkalies.

On their way to enter into the blood-current both the lymph and chyle undergo certain changes. Before passing through the lymphatic glands the fluid contains much fewer lymph corpuscles than after it has traversed the glands: from this fact and from the structure of the lymph glands we may conclude that they are the chief sources of these white cells. The chyle of the lacteal vessel of the mesentery contains particles of fat which greatly exceed in size those found in the thoracic duct, so we may infer that the fat emulsion undergoes a further subdivision or modification on its way through the glands.

The lymph which has been collected from the lymph channels of the extremities has been found to contain less albumin than that coming from the main trunk, and after long fasting the lymph from the thoracic duct has the same characters.

The lymph contains a considerable quantity of carbonic acid gas, about 50 vol. per cent., some of which is readily removed by the air-pump, and is therefore said to be merely absorbed by the fluid, and some of which can only be removed by the addition of acids, and is therefore considered to be in chemical combination. Only mere traces of oxygen have been found in the lymph.

The quantity of chyle and lymph poured into the blood varies so much that any estimation of the amount entering in a given time is unreliable.

The following circumstances upon which the variations may depend are instructive :—

1. The ingestion of liquid and solid food causes a great increase in the amount of chyle. This is obvious from the change in the state of the lacteal vessels, which from being transparent and almost empty become widely distended and white.
2. The activity of any organ causes an increase of lymph to flow from it.
3. Impediment to the return of the venous blood from any part increases the irrigation, *i.e.*, the lymph.
4. Increase of the amount or the pressure of the blood flowing through any part augments the lymph flow.
5. The administration of curare increases the amount of lymph.

The history of the structural elements or lymph corpuscles, which exist in such numbers in the large lymph channels, requires some further discussion, as these cells are composed of active protoplasm, and therefore must be destined for some important function, and are produced by some vital process.

The origin of the lymph corpuscle is not restricted to any one part of the body or to any special organ. It has been said already that the lymphatic glands are supposed to be the most important source of these cells, because the follicular tissue is filled with them, and the lymph contains a much larger number after it has passed through some lymph glands. In the lymphoid tissue of the spleen they are also very numerous, and no doubt many of them have their origin in that organ as well as in the intestinal follicular tissue and in the red marrow of the bones. Although their number is relatively small, lymphatic cells occur in the lymph channels that are unconnected with a lymphatic gland, and these cells no doubt come from the blood, which, as we shall see, contains many cell elements, which are actually the lymph cells poured into it from the lymphatic duct. These cells, when they arrive at the minute blood-vessels sometimes leave the vessels and creep by amœboid movements into the interstices of the tissue, along with the irrigation stream. They may permanently abide in the tissue, or they may be washed back into the larger lymph channels with the stream of surplus lymph. When the abnormal increase of activity of a tissue known as inflammation, occurs, this escape of the white cells from the blood takes place with great rapidity, and the stages in the process can be watched under the microscope.

Still another source of the lymph cells may be from proliferation of the cells which lie in the tissues. The fixed tissue-cells are said to be capable of producing cells identical with lymph cells, and by division possibly multiply and produce their like, which may be carried along by the lymph stream as lymph cells.

The enormous number of cells which accumulate as pus when an abscess forms are structurally identical with lymph cells, and probably arise from these combined sources, viz., escape from the blood-vessels and proliferation of the tissue cells.

The lymph cells therefore, whether they have their origin in a lymph gland, the spleen, or in connective tissue, perform a kind of circuit, going with the lymph into the blood, and are distributed with the latter to the tissues, whence they may be once more carried into the lymph stream.

Movement of the Lymph.

In some of the lower animals small muscular sacs occur in the course of the main lymph channels which pump the lymph into the great veins by contracting rhythmically much in the same way as the heart.

In man and the higher animals no such lymph-hearts have been found ; the onward movement of the fluid depends chiefly on the pressure with which the irrigation stream leaves the blood-vessels. The fluid in the blood-vessels, as we shall presently see, is under considerable pressure, which causes the plasma to leave the capillaries. Hence, if a lymphatic trunk be tied, there is intense filling of all its tributaries until a great pressure (8—10 mm., soda solution) is developed in the vessels.

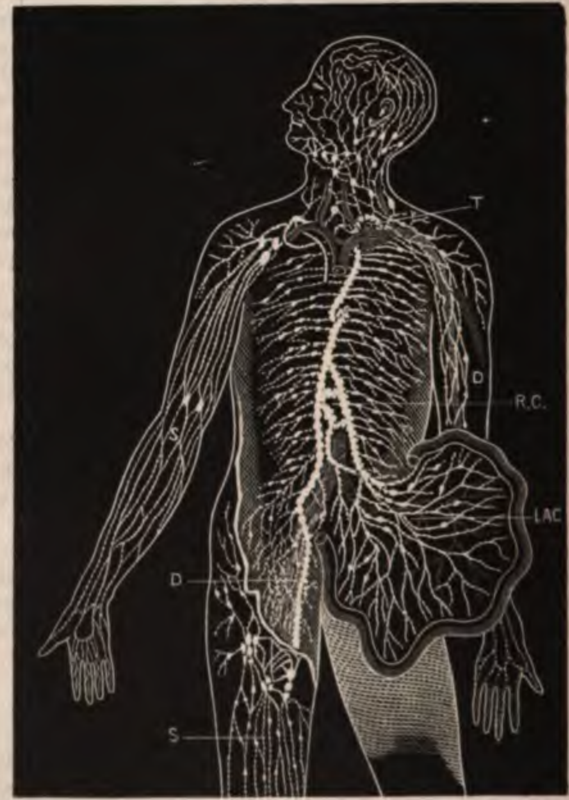


Fig. 94.—Diagram showing the Course of the Main Trunks of the Absorbent System. The lymphatics of lower extremities, &c., meeting the lacteals of intestines at the receptaculum chyli (R. C.), which opens into the thoracic duct. The superficial vessels are shown in the diagram on the left arm and leg (S.), and the deeper ones on the arm to the right (D.). The glands are here and there shown in groups. The small right duct opens into the veins on the right side. The thoracic duct discharges into the union of the great veins of the left side of the neck (T.).

While the pressure exerted on the small tributaries of the lymph channels is considerable, that in the thoracic duct is extremely small, for the following reasons. The blood in the large veins into which the duct opens is under less pressure than in any other part of the vascular system, owing to the thoracic suction, or absence of pressure in the thorax, caused by the elastic traction of the lungs. In fact, the pressure in the large veins, *e.g.*, brachial, &c., varies from 0 to −4 mm. Hg., and that in the venæ cavæ is always negative, except in forced expiration, and varies, according to the period of the respiratory rhythm, from −5 mm., in inspiration, to −2 mm. in expiration.

The fact that the lymph at the origin of the small channels is at a pressure of 8 to 10 mm. of water, whilst at the entrance to the vein it is nil, would be sufficient to explain the movement, even if there were no other force aiding its movement.

It must be remembered that every lymph vessel is furnished with closely set valves, which prevent the fluid it contains from being forced backwards, so that any accidental local pressure exercised on the exterior of a lymph channel helps the fluid onwards to the veins. Along their entire extent these vessels are subject to certain forces which must materially aid the flow of the lymph stream. The first of these is the pressure exerted on the small vessels by the movement of the muscles in the neighbourhood. The second is the unequal distribution of atmospheric pressure, which has full force on the peripheral channels, but is kept off the thoracic duct and its termination, as already mentioned, by the rigidity of the thoracic wall, which, together with the tendency of the elastic lungs to shrink, causes a permanent negative pressure in the thoracic cavity through which the duct passes. And lastly, the thin-walled lymphatics are everywhere surrounded with very elastic textures enclosed in an elastic skin, which exert an amount of pressure, sufficient to empty and press together the walls of the vessels after death, and therefore during life must have considerable influence upon the fluid they contain.

The movements of the chyle depend on the same forces, with the addition of the power used in the contraction of the villi, which pump the chyle from the lacteal radicles into the network of valved vessels in the submucous tissue.

The commencement of the thoracic duct is, moreover, placed in the abdominal cavity, and therefore is constantly under the influence of the positive pressure exerted by the abdominal wall on the contained viscera. The rest of the duct is in the thorax, where the pressure is habitually negative, but where certain variations coincident with inspiration and expiration take place, which must aid the onward flow of fluid in a vessel containing valves so closely set.

CHAPTER XIII.

THE CONSTITUTION OF THE BLOOD AND BLOOD PLASMA.

In all animals, except those which form the lowest class (Protozoa), the distribution of the nutritious materials to the various parts of the body, as well as the collection of the effete matters prior to their expulsion, is carried on by the medium of a fluid which circulates through the different parts of the body. This fluid is the blood.

In vertebrate animals the blood passes through a closed system of elastic pipes and it is kept in constant motion by the action of a muscular pump. It is first forced through strong-walled branching canals called arteries, whose walls gradually become thinner as the branches get smaller, and these end in a network of delicate channels (capillaries), through which it slowly trickles into the wide soft-walled veins by means of which it flows gently back again to the heart. In its course it receives the nutritive materials from the stomach and intestines after digestion, the specially elaborated substances from the liver, spleen, and lymph glands, and the oxygen absorbed from the air in the lungs. In short, it contains and bears to their destination all the materials required for the chemical changes of the various tissues. While passing through the capillary networks of the various tissues, it takes up the waste materials resulting from the tissue changes and bears them to their proper point of exit from the body; at the same time the nutriment is allowed to ooze through the delicate vessel walls and be diffused in the tissues.

General Characteristics of the Blood.

The blood of vertebrate animals is of a bright scarlet colour when exposed to the oxygen of the air, but when not in contact with oxygen it is a dark purplish red.

The blood is remarkably opaque, as may be seen by placing a thin layer on a piece of glass over the page of a book. This opacity depends on the fact that the blood, as will presently be seen, is not a red *fluid*, but owes its colour to the presence of solid red particles or corpuscles which float in a clear pale fluid. The blood has a peculiar smell (halitus) distinct in different animals and man, dependent on certain volatile fatty acids. Its specific gravity varies from 1045 to 1075, the average being 1055. The solid parts (corpuscles) are heavier (sp. gr. 1105) than the liquor sanguinis (1027).

When first shed the blood has a slippery feel, which it soon loses, becoming sticky as it passes through the various stages of the process of coagulation.

AMOUNT OF BLOOD IN THE BODY.

The total amount of blood has been estimated to be from $\frac{1}{13}$ to $\frac{1}{14}$ of the body-weight for an adult man, and somewhat less for a new-born child.

Much difficulty has been found in arriving at an accurate estimation of the amount of blood in the body. In the first place, all the blood cannot be made to flow out of the vessels of an animal when it is killed. Secondly, the quantity and quality of blood are constantly varying with the capacity of the blood-vessels. Thirdly, when slowly withdrawn from the body during life it is rapidly replaced by more fluid passing into the blood vessels. This explains the enormous quantity of blood occasionally reported to be shed in cases of bleeding to death. In these cases, as quickly as the blood is lost, fluid is absorbed by the fine vessels to replace it, so that if the bleeding be gradual the standard quantity is still kept up in the vessels. Thus the very sudden loss of a comparatively small quantity of blood may cause death, whereas, if the bleeding go on sufficiently slowly and gradually, as much or even more in quantity than normally exists in the entire body may escape without fatal result, but of course much of this is fluid which has recently entered the vessels to replace the blood already lost.

Weber's Method.—The per centage of solid matters in the blood is first carefully estimated. The absolute quantity of solids in the drawn blood is then ascertained and added to the solids obtained by washing out the blood-vessels. Here the error arises from the fact that, in washing out the blood-vessels, much solid matter besides that belonging to the blood is taken from the tissues and thus an excess is found.

Valentine's Method.—A small quantity of blood is drawn from a vein and measured and its per centage of solids is accurately estimated; thereupon a known quantity of water is injected into the vessels. After some time being allowed for proper distribution of the water a sample of the diluted blood is taken and its solids estimated. The difference in solid contents of the two samples shows the degree ot dilution caused by a known quantity of water introduced into blood of ascertained strength, and thus the amount of the fluid diluted (the blood) may be calculated and added to the amount of the first sample of blood.

This method cannot give accurate results, because in the time necessary for the distribution and mixture of the water with the circulating blood much of the former is excreted by the kidneys and skin, and the second sample of blood is more concentrated than should result from such dilution.

Welcker's Method depends upon the estimation of the colouring matter of the blood. He connected the carotid with a small T piece, and allowed the animal to bleed into a bottle in which the blood could be defibrinated by shaking with pieces of glass. One cubic centimetre of this defibrinated blood was carefully measured off and saturated with carbon mon-oxide (CO), which gives a permanent and equally bright red colour. It was then diluted with 500 c.c. distilled water and kept as a standard colour-solution. The blood-vessels of the animal were then washed out with ·6 per cent. solution of sodium chloride until the solution flowing from the jugular vein was colourless. The tissues of the animal were then chopped up and steeped in water and pressed. The washings of the vessels and the infusion from the tissues were added together and diluted until they had the same colour-intensity as a layer of the standard solution of the same thickness. Every 500 c.c. of these diluted washings corresponds to 1 c.c. of blood.

By this method the following estimates have been made of the relation of the blood to the body weight :—

Mice	$\frac{1}{12}$—$\frac{1}{13}$
Guinea Pig	$\frac{1}{17}$—$\frac{1}{22}$
Rabbit	$\frac{1}{15}$—$\frac{1}{22}$
Dog	$\frac{1}{11}$—$\frac{1}{18}$
Cat	$\frac{1}{21}$
Birds	$\frac{1}{10}$—$\frac{1}{13}$
Frog	$\frac{1}{15}$—$\frac{1}{20}$
Fish	$\frac{1}{4}$—$\frac{1}{19}$

Only approximate estimates of the distribution of blood in the body during life can be made, since there can be no accurate method of investigation, and the amount varies enormously according as the organ or part is in a state of rest or activity. It is supposed that a quarter of the entire amount is habitually flowing through the heart and great vessels, a quarter in the skeletal muscles, another quarter in the liver, and in all the other parts only a fourth.

PHYSICAL CONSTRUCTION OF THE BLOOD.

As already stated the blood is not a red fluid. It is seen with the microscope to be made up of a clear fluid called *plasma* or *liquor sanguinis,* which contains an immense number of little disc-shaped bodies called red corpuscles and a few colourless protoplasmic cells, which are called white corpuscles ; so that the living blood may be physically tabulated, giving approximately an estimation of the relative amounts, thus:—

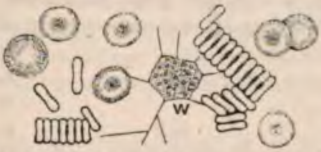


Fig 95.—Human Blood after death of the elements. The red corpuscles are seen in different positions showing their shape, some also are seen in rolls. Only one white cell (w) is seen, misshapen and entangled in fibrin threads.

$$\text{Blood}\begin{cases}\text{Plasma or Liquor Sanguinis———}\frac{3}{5}\\ \text{Solid or Corpuscle}\left\{\begin{matrix}\text{Red discs}\\ \text{Pale cells}\end{matrix}\right\}\text{—}\frac{2}{5}\end{cases}$$

PLASMA.

The fluid part of the blood is of a pale straw colour, when pure and free from the colouring matter of the blood corpuscles, and of slightly less density than the blood corpuscles, (v. p. 169). Except special precautions are taken the plasma is altered when removed from the blood-vessels and coagulation of the blood takes place, so that under ordinary circumstances plasma does not come under observation, except when the constitution of the blood is revealed by the microscope. It was first separated from the corpuscles by the filtration of frog's blood to which had been added strong syrup, which checks coagulation and spoils the flexibility of the corpuscles, so that they are caught in the meshes of the filter and the clear plasma passes through.

To obtain mammalian plasma free from corpuscles it is necessary to use some other method, as the small elastic corpuscles easily run through the meshes of the thickest filter-paper.

The blood of the horse is chosen because it coagulates more slowly than that of most mammals, and delay in the coagulation or postponement of the change in the plasma is the chief object to be obtained. To encourage this delay the blood is drawn from a vein into a cylinder surrounded with a freezing mixture. The cold, however, must not be so intense as to absolutely freeze the blood, for the wished for subsidence of corpuscles could not go on if the blood becomes solid. It is then left quite motionless for 24 hours, after which time it will be found that the heavy corpuscles have fallen and left a clear supernatant fluid, which is plasma containing some white cells. This can be removed with a cool pipette and passed through an ice-cold filter to remove the cells, then tolerably pure plasma is obtained which soon cogulates at the ordinary temperature.

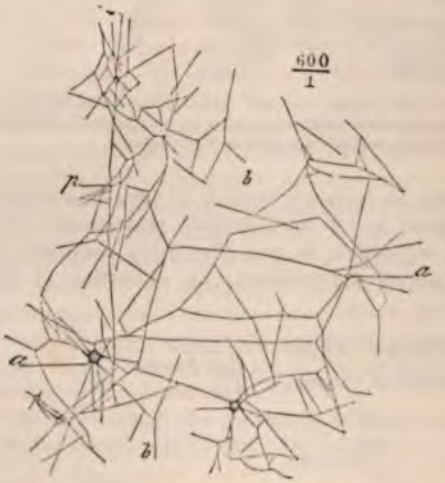


Fig. 96.—Reticulum of Fibrin Threads after staining has made them visible. The network (*b*) appears to start from granular centres (*a*). (Ranvier.)

Another method of checking coagulation consists of letting the blood flow into a 25 per cent. solution of magnesium sulphate (about three volumes of blood to one of the solution). This, if left in a cool place, will not coagulate, and the corpuscles will separate by subsidence from the plasma and salt solution, which form an upper layer of clear fluid. If the salt be removed by dialysis or weakened by dilution with water, coagulation commences.

The coagulation of plasma can be seen with the microscope to depend upon the appearance of a close feltwork of exquisitely delicate finely granular elastic fibrils which pervade the entire fluid and cause it to set into a soft jelly. The substance forming the meshes is called *fibrin*.

Some time after the plasma has gelatinised, the threads of fibrin break away from their attachment to the vessel in which the coagulum is contained, and owing to their elasticity the general mass of fibrin contracts, squeezing out of its meshes clear drops of fluid termed *serum*.

The fibrin clot gradually shrinks into unappreciable dimensions, and floats in the abundant fluid serum.

The separation of the serum is accelerated by agitation of the soft clot; and if brisk agitation, such as whipping, be kept up for a few minutes the plasma does not form a jelly, but the fibrin firmly adheres to the stirring rods and at once contracts around them.

CHEMICAL COMPOSITION OF PLASMA.

On account of the rapid spontaneous formation of fibrin and serum when the plasma is removed from the body and allowed to die, the exact chemical condition of the liquor sanguinis during life cannot be investigated, the separation occurring before the simplest chemical method can be carried out.

We have no reason to suppose that fibrin exists normally in the blood, but it would appear that this substance is only formed at the moment of coagulation, and is one of the most obvious of many changes which take place at the time of the death of blood plasma.

The chemical change comprehended under the term coagulation occurring when plasma is deprived of its means of vitality, and ending in the production of fibrin and serum, is naturally of the first importance in studying the chemical relationships of living plasma. It can best be followed out in the coagulation of plasma when separated from the corpuscles, for (although the stages in the coagulation of blood are the same, the appearance of an insoluble albumin —fibrin—being the one essential in either case), the corpuscles complicate the process and modify the appearance of the clot.

Not only is the fibrin not present as such in the living plasma, but it requires for its production the presence of other substances which either do not exist in the living plasma, or are there so chemically associated as not to bring about the change which occurs when the plasma is dead.

The reasons for believing this are the following. Fluids which sometimes collect by a slow process in the serous cavities of the body, *e.g.*, hydrocele fluid, pleural effusion, &c., if kept quite clean do not generally undergo spontaneous coagulation. If to one of these some serum from around a blood clot be added, coagulation takes place just as in plasma (Buchanan). That is to say, we have here two fluids, neither of which coagulates when left to itself, but which do coagulate when mixed together. From each of these fluids a substance can be precipitated by passing a stream of carbon dioxide (CO_2) through the fluids. Both precipitates readily re-dissolve in weak saline solutions.

The solution prepared from the hydrocele fluid causes blood serum to coagulate; that prepared from the blood serum causes the hydrocele fluid to coagulate; and when mixed together the mixture of the two solutions coagulates; while the serum and hydrocele fluid from which the substances have been removed no longer have the power of exciting coagulation in each other or in like fluids. Here, then, are brought to light two materials: one, which may be obtained in considerable quantity from serum after coagulation, is called serum-globulin or paraglobulin, the other occurring in serous fluids is named *fibrinogen*. Both of these substances are present in the dying plasma of the blood prior to coagulation. They can be obtained both together from the plasma (when either of the precautions already mentioned—viz., the application of cold, or the addition of neutral salt — has been taken to prevent the formation of fibrin) if the plasma be treated with sodium chloride to saturation. This precipitates a substance which readily dissolves if water be added to weaken the salt solution, and after some time the solution undergoes spontaneous coagulation, while the plasma from which it has been made has lost that power. This *plasmin* (Denis) no doubt is made of different globulins, chiefly serum-globulin, and fibrinogen, and contains in itself all the necessary "factors" of fibrin formation, but is not at all identical with fibrin, since it readily dissolves in weak saline solutions, like the class of proteids called globulins, while fibrin is quite insoluble in such solutions.

In plasma removed from its normal relationships, then, both serum-globulin and fibrinogen exist; but the former in far greater quantity than the latter, since the serum, after the blood clot is formed, contains no more fibrinogen, while the serum-globulin or paraglobulin makes up nearly half the entire solids of the remaining serum.

In preparing fibrinogen and paraglobulin (or, as he called the latter, *fibrinoplastin*) Schmidt found that the more carefully they were made, the weaker and more uncertain their action as fibrin factors became; and finally he made solutions which, when added together, did not produce coagulation, but which, when added to less pure solutions, gave good firm clots. From this he suspected that a third agent which acted as a ferment was necessary to put into operation the fibrin-producing properties of the other two factors. He moreover succeeded in separating the third agent, to which he gave the name of *fibrin-ferment.* By treating blood serum with twenty times its volume of strong alcohol and allowing it to stand a month or two, the proteids are precipitated and rendered quite insoluble in water, and with them the ferment is carried down. From the dried and powdered precipitate the ferment is extracted with water. This solution when added to the mixture of the pure fibrin factors which by themselves did not coagulate caused rapid coagulation, but not when added to either one or the other of them singly (Schmidt).

This material seemed to have been influenced by those circumstances which affect the activity of ferments in general: it has a minimum, 0° C., maximum, 80° C., and optimum, 38° C. temperature of activity, with various gradations of rapidity of action between each, and it is destroyed by a temperature above 80° C. The amount of fibrin-ferment only seems to influence the rapidity with which the fibrin is formed, not the amount, which rather depends on the quantity of serum-globulin (paraglobulin).

The source of the three fibrin generators is a question of much difficulty, and may be discussed with more profit, together with the question of blood coagulation, within and without the vessels, after the morphological elements have been described.

Preparation and Properties of Fibrin.

Fibrin may be procured either from plasma or blood by whipping and then washing the insoluble fibrin with water. When fresh it has a pale yellow or whitish colour, a filamentous structure, and is singularly elastic. It is not soluble in water, weak saline solution, or ether. Alcohol makes it shrink by removing its water. When quite dry it is brittle and hard, and can be reduced to a powder. It swells in 1 per cent. hydrochloric acid, and if then warmed is soon converted into acid albumin.

The amount formed varies very much even in the blood drawn from the same animal at the same time, but is always very small compared with the size of the blood clot. It never reaches as much as 1 per cent., commonly varying from 0·1 per cent. to 0·3 per cent. of the entire mass of blood.

SERUM.

This name is given to the clear fluid which oozes out of the clot of plasma. It only differs from the latter in its chemical composition in so far that fibrin is separated from it. Though chemically this is a slight difference it signifies the change from a complex living body (blood plasma) into a solution of dead albumins, &c.

Serum is a clear straw-coloured alkaline fluid of 1028—1030 sp. gr., holding in solution different organic substances and some inorganic salts. After a full meal the serum is said to be more or less milky from the presence of finely divided fat.

It contains about 9 per cent of solid matters, of which a large proportion, 7 per cent., are proteids. Of these the most abundant is (1) serum-albumin (about 4 per cent. in man), a solution of which becomes opaque at 60° C., and coagulates at a heat of 73°—75° C. The proteid next in importance is (2) serum-globulin or paraglobulin (about 3 per cent. in man), which has already been mentioned. It may be precipitated imperfectly by CO_2, or completely by magnesium sulphate. (3) Serum casein has been obtained from serum by careful neutralisation with acetic acid after the removal of the paraglobulin by CO_2. This is said to be paraglobulin which has failed to come down with the CO_2. (4) Neutral fats in a state of fine subdivision are present in a variable quantity; also (5) lecithin; (6) traces of sugar; (7) various products of tissue change—kreatine, urea, &c.; and (8) inorganic salts, viz., sodium chloride, about 5 per cent., and sodium carbonate, which probably existed in the blood as sodium hydric carbonate. There is also a small quantity of potassium chloride. But it should be remembered that there is about ten times more sodium than potassium salts in the serum, and probably in the blood plasma.

CHAPTER XIV.

BLOOD CORPUSCLES.

THE relative number of red discs to the colourless cells is said to be, on the average, 350 to 1. This is true of the blood drawn from the fine vessels by puncture. While in the vessels the blood must contain a greater proportion of the colourless cells, for by the ordinary method of obtaining blood for examination, they do not flow out of the punctured capillaries as readily as the red discs, and moreover many of them become disintegrated very shortly after they are removed from the circulation. Although the number of red discs normally alters but little, the relative number of red to white varies very much on account of the constant changes occurring in the number of the white cells, which has been found to differ according to the observer, the situation, and other circumstances, as shown in the following table, which gives the number of red corpuscles to one colourless cell :—

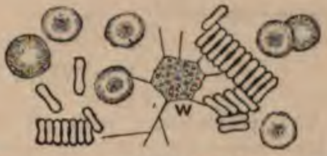


Fig. 97.—Human Blood after death of the elements. The red corpuscles are seen in different positions showing their shape, some also in rolls. Only one white cell (w) is seen, misshapen and entangled in fibrin threads.

Observer's estimate of normal proportion :—	Red. White.
Welcker	335—1
Moleschott	357—1
In various parts of the circulation :—	
Splenic vein	60—1
Splenic artery	2260—1
Hepatic vein	170—1
Portal vein	740—1

According to age or sex :—	Red. White.
Girls	405—1
Boys	226—1
Adult	334—1
Old age	381—1

According to general conditions :—	
When fasting	716—1
After meal	347—1
During pregnancy	281—1

In a disease of the spleen and lymphatic glands called Leucocythemia there may appear to be nearly as many white cells as red discs. Here, however, the red discs are deficient, while the colourless cells are multiplied.

THE WHITE BLOOD-CELLS.

The protoplasmic cells of the blood, commonly called the white corpuscles, differ in no essential respect from the pale round cells which are found in most of the tissues of the body. They exist in great numbers in the fluid which drains back from the tissues into the blood, namely, the lymph, and occupy a great part of the lymphatic glands and spleen. They are often spoken of as lymphoid cells, leucocytes, or indifferent formative cells, on account of their being so widely distributed throughout the tissues.

When fresh blood is examined with the microscope these cells can be seen generally adhering to the glass slide or cover-glass and lying singly, apart from the groups of red discs. They can be recognised by their faintly bluish hue or absence of marked colour, their finely granular structure, spherical shape, and the nuclei which may often be recognised near the centre of the cell. Though not always visible in quite fresh preparations, the nuclei can be brought to light by the action of many reagents—*e.g.*, acetic acid. If looked at while being moved by the blood-current in the capillary vessels, they are seen to pass slowly along in contact with the vessel wall, while the red corpuscles rush rapidly past them down the centre of the channel (fig. 98). This may partly be due to their peculiar adhesiveness, which also causes them to stick to the glass slide, whilst the red discs are washed away when a little stream of saline solution is allowed to flow under the cover-glass. These cells show all the manifestations of activity characteristic of independent living beings. If kept in a medium suitable to them, and at the temperature of the body, they will be seen soon to alter their appearance; their outline becomes faint, they are no longer spherical, but very irregular in shape, and constantly change their form by sending out and retracting delicate processes, by means of which they change their position, so that they may be said to perform locomotion. These movements are rendered more active by a slight increase of temperature, and are checked by cold. For continued observation about 38° C. is the best temperature. They respond to many other influences, such as electricity, &c., even for a considerable time after removal from the body.

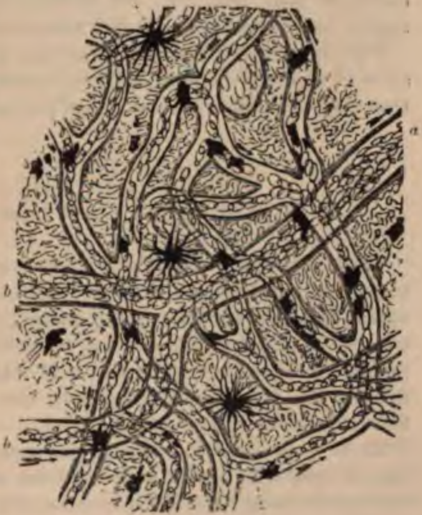


Fig. 98.—Vessels of the Frog's Web.

(*a*) Trunk of vein, and (*b b*) its tributaries passing across the capillary network. The dark spots are pigment cells.

No doubt they absorb fluid nutriment continually from the surrounding medium, as is shown by the effect of poisons on them; and, by the repeated contractions and relaxations of parts of their substance in the form of pseudopodia, they appear to take into the inner parts of the protoplasm solid particles, which after some time are ejected after the manner of the small unicellular animals known as amœbæ (IV., p. 60).

While in motion in the circulation none of these amœboid movements appear to take place, but when an arrest of the flow of blood in the capillaries occurs they not only change their form, but also their position; and if there be no onward flow of blood for some little time, they creep out of the capillaries, passing through the delicate vessel-walls. This emigration of the blood cells is possibly a common event when a tissue is in need of textural repair. When excessive it forms one of the most striking items of the series of events occurring in inflammation.

These cells differ much in size; generally they are somewhat larger than the red discs. Nothing like a cell-wall can be seen to surround them, and from the movements above described it would appear certain that they are free masses of active protoplasm.

The number of white cells that can be collected is too small to allow of accurate chemical analysis, but there is no reason to suppose that they differ from other forms of protoplasm.

ORIGIN OF THE COLOURLESS BLOOD-CELLS.

Since such an unimportant circumstance as a hearty meal can materially influence the numbers of the white corpuscles, it would appear that they must be usually undergoing rapid variations in their number—probably by their being constantly used up and periodically replaced by new ones. The places in which they occur in greatest number are the lymphatic glands, the spleen, and the lymph follicular tissue in the intestinal tract.

There is no doubt that the lymph contains a much larger proportion of these cells after it has passed through the lymph glands, and the blood coming from the spleen contains an excessive proportion of them.

It is then not unreasonable to suppose that many of the white cells found in the blood have their origin in these organs.

They may also be developed from similar cells in any tissue, but their multiplication by *division*, other than that which probably occurs in the lymph follicles where it cannot be seen, is a circumstance of the greatest rarity, and few observers have been fortunate enough to witness the phenomenon.

The destiny of the white blood cells is probably manifold. From the readiness with which they escape from the capillaries and wander by their amœboid movement through the neighbouring tissues to reach any point of injury, it would appear that they take an active part in the repair of any tissue whose vitality has in any way suffered. During the growth of all tissues the cells seem to contribute active agents in their formation; thus in the formation of bone it has been stated that escaped blood cells or their immediate offspring help to lay down the calcareous material, and some even settle themselves as permanent inhabitants of the lacunæ.

Further, they are in all probability the means of renewing the red discs. Their protoplasm either takes up the colouring matter from its surroundings, or forms it within itself from suitable ingredients. Certain it is that cells are found which are recognisable as white blood cells which have more or less of the red colouring matter embedded in their substance. As this increases the cell gradually loses its distinctive characters and assumes those of a red corpuscle. Such elements, it will be seen, are common in the spleen and the blood leading from it.

The Red Corpuscles.

The red discs were discovered in the human blood by Leuwenhoek, about 1673. They alone give the red colour which characterises the blood of all vertebrated animals (except the amphioxus), but are not found in the blood of the invertebrata, which only contains colourless cells. When the blood of the invertebrates has a colour, it owes it to the fluid, not to the corpuscles. The individual discs when viewed singly under the microscope appear to be pale orange, but when in masses the red becomes apparent.

The shape of the corpuscles differs in different classes of animals. In man and all mammalia they are discs which are concave on each side, and rounded off at the margin. The only class of mammals which form an exception to this rule are the camalidæ, whose red corpuscles are elliptical in shape, like those of all non-mammalian vertebrates.

The corpuscles of birds, amphibia and fish are flattened elliptical plates, which are slightly convex on each side, and contain a distinct oval nucleus in their centre.

The size of the corpuscles varies greatly in different classes of animals, but is strikingly constant in the same class. A glance at the following diagram, in which the corpuscles are drawn to scale, will give an idea of their relative sizes in examples of the different classes of animals, and will make the following points more rapidly obvious than any description.

The size of the animal has no general relation to the size of the corpuscles. The human red discs are of a fair average size when compared with those of other mammals, and therefore man's blood cannot be distinguished from that of the other mammalia.

The mammalian corpuscles are, on the whole, small when compared with those of the other vertebrates. The batrachians are distinguished by the great size of the corpuscles. Those of the Amphiuma Tridactylum are visible to the naked eye.

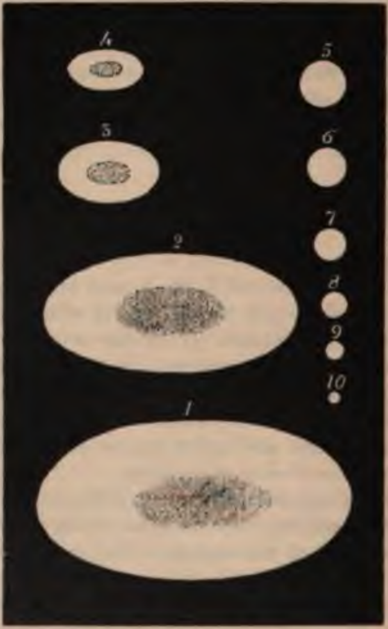


Fig. 99.—Diagram of the relative sizes of red corpuscles of different animals. The measurements below are in fractions of an inch.

1.	Amphiuma	[illegible] × [illegible]
2.	Proteus	[illegible] × [illegible]
3.	Frog	[illegible] × [illegible]
4.	Pigeon	[illegible] × [illegible]
5.	Elephant	[illegible]
6.	Man	[illegible]
7.	Dog	[illegible]
8.	Horse	[illegible]
9.	Goat	[illegible]
10.	Muskdeer	[illegible]

The following measurements are given by Welcker for the human discs :—

Diameter . . . 0·0,077 of a millimetre = $\frac{1}{3200}$th of an inch.
Thickness . . . 0·0,019 of a millimetre = $\frac{1}{12400}$th of an inch.
Volume . 0·000,000,077 of a cubic millimetre.
Surface . . . 0·000,128 of a square millimetre.

The last measurement would give about 2,816 square metres for the entire blood of an adult. A surface of 11 square metres is exposed every second in the lungs for the absorption of oxygen.

When circulating in the vessels, or immediately after removal, the red corpuscles are very soft and elastic, being bent and altered in shape by the slightest pressure, and easily stretched to twice their diameter. But the moment pressure or traction is removed, they return to their normal biconcave disc-shape if the medium in which they lie continue of the normal density. (See fig. 97, p. 177.)

Changes take place in the blood shortly after it is removed from the body, which seem to be associated with the loss of function (death) of the red discs, as shown by their rapid destruction if re-introduced into the circulation.

These changes are checked by cold, and facilitated by heat, a temperature above that of the body causing them to take place almost immediately. Associated with the loss of function of the discs is observed a change accompanied by an apparent increase of adhesiveness, which causes them to stick together, commonly adhering by their flat surfaces, so as to form into rolls, like so many coins placed side by side. That this adhesion is not a mere physical process, independent of the chemical properties of the corpuscles themselves, seems proved by the following facts :—(1) It does not occur immediately when the blood is drawn, and it disappears after a certain time without the addition of re-agents; (2) while the blood is in the living vessels under normal conditions there is no adhesion, but it soon appears when any standstill in the circulation takes place—as in inflammation; (3) it does not occur when saline solutions are added to the blood. It seems then to be dependent upon a peculiar property of the discs, which only exists for a time coincident with the changes that accompany the appearance of fibrin.

The shape of the discs changes when the density of the medium in which they are suspended is altered. When the density is reduced, as by the addition of water, they swell and become spherical, and break up the rouleaux, the colouring matter at the same time becoming dissolved in the medium. (Fig. 100.) When the density is increased by slight evaporation, or the addition of salt solution about 1 per cent. they cease to be concave, and become *crenated* or spiked like the green fruit of the horse-chestnut. (Fig. 101.) The addition of strong syrup causes the corpuscles to shrivel and assume a great variety of peculiar bent or contorted forms. (Fig. 102.) Elevation of temperature or repeated electric shocks causes peculiar changes in shape, but since the change is associated with the death of the element, it cannot be attributed to vital activity comparable with that which is seen in the white cells.

The discs show no signs of structure under the microscope : they look perfectly homogenous transparent bodies of a pale orange colour, all efforts to demonstrate the limiting membranes, formerly supposed to surround them, having failed. Their behaviour when certain reagents are added to the blood shows that the corpuscles have two constituents: (1) the colouring matter, *Oxyhæmoglobin*; and (2) the *Stroma*. The colouring matter may be removed—as above stated, by water—from the corpuscle, and then leaves a perfectly colourless transparent foundation or groundwork, which appears to be in some way porous, so as to hold the colouring matter in its interstices. The effect on the naked-eye appearance of the blood produced by the removal of the colouring matter from the stroma is to alter the colour and increase the transparency of the fluid. The oxyhæmoglobin now forms a transparent dark-red *lakey* solution, and the corpuscles, being quite colourless, are practically invisible. This transparency of the fluid does not depend on any change in the oxyhæmoglobin, but merely on its being dissolved out of the discs. This process, which is commonly spoken of as rendering the blood "lakey," may be brought about by the following means. (1) The addition of about ¼ its bulk of distilled water, to dissolve the colouring matter out of the stroma, which may then be rendered obvious by a weak solution of iodine. (2) By the addition of chloroform, ether, neutral alkaline salts, or alkalies. (3) By passing repeated strong induction shocks through the blood. (4) By rapidly freezing and thawing the blood several times.

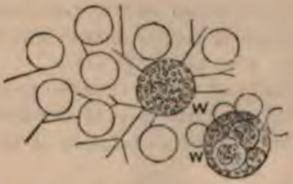


Fig. 100.—Microscopic appearance of the blood after the addition of distilled water. Red Corpuscles become colourless or pale, separate, and spherical. The white are seen to be swollen round and granular with clear nuclei.

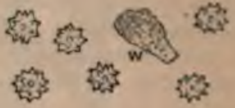


Fig. 101.—Showing effect of evaporation. Six Red Corpuscles crenated. (w) White cell changing shape.

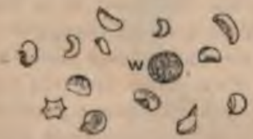


Fig. 102.—Red Corpuscles, shrivelled by the addition of strong syrup. (w) White Corpuscle.

All of these processes produce the same effect; viz., the red matter leaves the stroma intact. Solutions of urea, bile acids, and heat of about 60° C. seem to destroy the discs, and thus remove the colouring matter. Carbolic, boracic, and tannic acids cause the colouring matter to coagulate and localise itself either at the centre or margin of the corpuscle. (Fig. 103.)

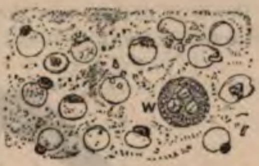


Fig. 103.—Blood Corpuscle after the addition of tannic acid.

The number of discs in the blood of man is enormous, namely, in a cubic millimetre of blood, about 5 millions for males, and 4½ millions for females, or about 250,000 millions for one pound of blood. The number varies much, not only in disease, but also as a result of the many physiological processes, such as changes in the amount of plasma, brought about by pressure-differences, &c.

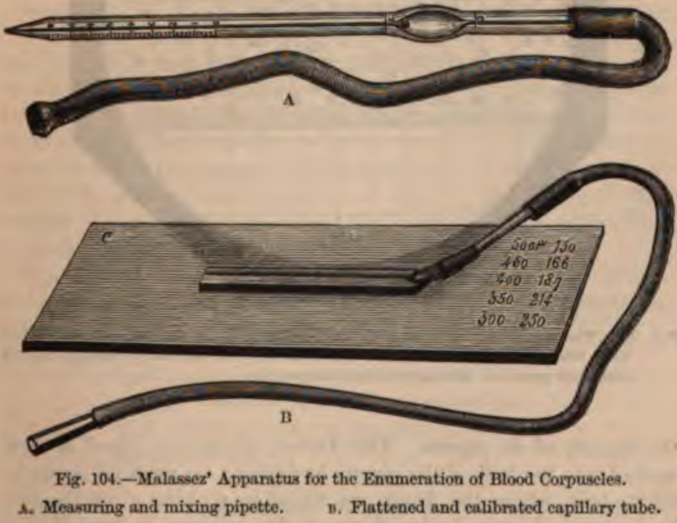


Fig. 104.—Malassez' Apparatus for the Enumeration of Blood Corpuscles.

A. Measuring and mixing pipette. B. Flattened and calibrated capillary tube.

In order to count the corpuscles the following method is employed. The blood is diluted with artificial plasma to 100 or 1,000 times its volume, and the corpuscles in a portion of the mixture carefully measured off by a capillary tube, and counted. This operation requires great care and delicate apparatus. One of the best-known methods is that of Malassez, the details of which are as follow :—

Blood is drawn into the capillary tube of a specially prepared delicate pipette (Fig. 104, A) up to a mark which indicates $\frac{1}{100}$ part of the capacity of the pipette. This known quantity of blood is then washed into the bulb of the pipette by drawing up artificial serum to fill the bulb, where the fluids are mixed by shaking about the fine bead contained in the bulb. Some of this mixture is then allowed to pass into a flattened capillary tube of known capacity fixed on a slide, and the number of corpuscles in a given length of this tube at two or three places is carefully counted. The important question, how much oxyhæmoglobin exists in a given sample of blood, can be determined by diluting a drop until the colour equals that of a standard solution of known strength.

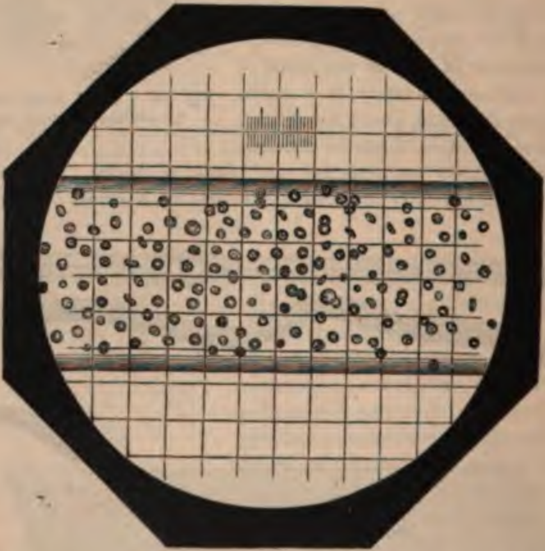


Fig. 105.—The appearance presented by the Capillary Tube of Malassez' Apparatus when filled with diluted blood and examined under a microscope magnifying 100 diameters provided with an eye-piece micrometer.

Chemistry of the Colouring Matter of the Blood.

Of the chemical constituents found in the red blood corpuscles, the red colouring matter is by far the most important. To it alone the blood owes one of its most important functions—the respiratory.

Oxyhæmoglobin is a chemical compound of great complexity, and of which the per centage composition is given as—

Carbon	53·85
Hydrogen	7·32
Nitrogen	16·17
Oxygen	21·84
Sulphur	·39
Iron	·43

Its rational formula is unknown, but the following has been proposed as approximate, $C_{600}\ H_{960}\ N_{154}\ Fe\ S_3\ O_{179}$. It is commonly regarded as a form of globulin, associated with a coloured material containing iron, called Hæmatin. Its chief peculiarities are (1) that although it contains a colloid substance, it crystallises more or less readily in all vertebrates when removed from the stroma of the corpuscles; (2) the considerable amount of iron it contains (0·4 per cent.); (3) the remarkable manner in which it is combined with oxygen to form an unstable compound; and (4) the ease with which it yields its oxygen to the tissues and takes it from the air.

The readiness with which the *oxyhæmoglobin crystals* are formed varies much in different animals and under different circumstances, as may be seen from the following list—

Most readily—guinea pig, rat, mouse.
Readily—cat, dog, horse, man, ape, rabbit.
With difficulty—sheep, cow, pig.
Not at all—frog.

The presence of oxygen causes the crystals to form more rapidly, so that a stream of oxygen passed through a strong solution of hæmoglobin causes small crystals of oxyhæmoglobin to form.

The crystals always belong to the rhombic system, being most commonly plates (man, &c.) and prisms (cat), and rarely tetrahedra (guinea pig) and hexagonal plates (squirrel).

The colour of the crystals and their solution vary according to the light by which they are looked at. By reflected light they are bluish red or greenish in colour, and by direct light, scarlet.

The *preparation* of *oxyhæmoglobin* crystals is accomplished by first separating the colouring matter from the corpuscles by freezing, or the addition of water or ether, and rendering it less soluble by evaporation, cold, and the addition of alcohol.

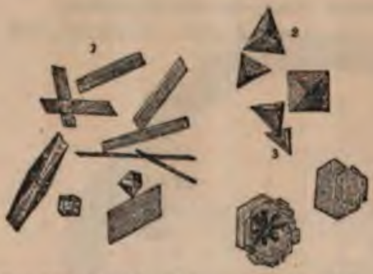


Fig. 106.—Crystals of Hæmoglobin from different animals, showing the variety in form of crystals—1, guinea pig; 2, man; 3, squirrel.

For microscopic observation it generally suffices to kill a rat with ether, and expose a drop of the blood diluted with distilled water on a slide until half dried, and then cover. Crystals appear in the fluid as it becomes more concentrated.

The combinations which hæmoglobin enters into are numerous, and throw much light upon the function of the corpuscles.

As already stated, the colouring matter, when exposed to the air, combines with oxygen to form a loose chemical compound called oxyhæmoglobin. This is the condition in which the colouring matter of the blood is commonly met with. Although so prone to combine with oxygen, the oxyhæmoglobin very readily parts with some of it. In the circulation it is always united with oxygen, normally leaving the lungs in a state of saturation. On its way through the capillaries of the tissues, it parts with some of its oxygen, becoming more or less reduced (hæmoglobin), but even the most venous blood always contains some oxyhæmoglobin.

The oxygen can be removed by reducing the pressure under an air pump, or by exposing the solution to a mixture of nitrogen and hydrogen. Various reducing agents rob the oxyhæmoglobin of its oxygen; and if blood or a solution of oxyhæmoglobin be sealed in a glass tube so as to exclude the air, the loose oxygen is taken up by some of the other constituents of the blood, and the oxyhæmoglobin becomes gradually reduced to hæmoglobin. This depends on the putrefactive changes in the proteids, and may be prevented by careful aseptic precautions. If the reduced hæmoglobin be shaken for a few moments with air, the bright colour characteristic of oxyhæmoglobin soon reappears, and if the reducing agent be not in-

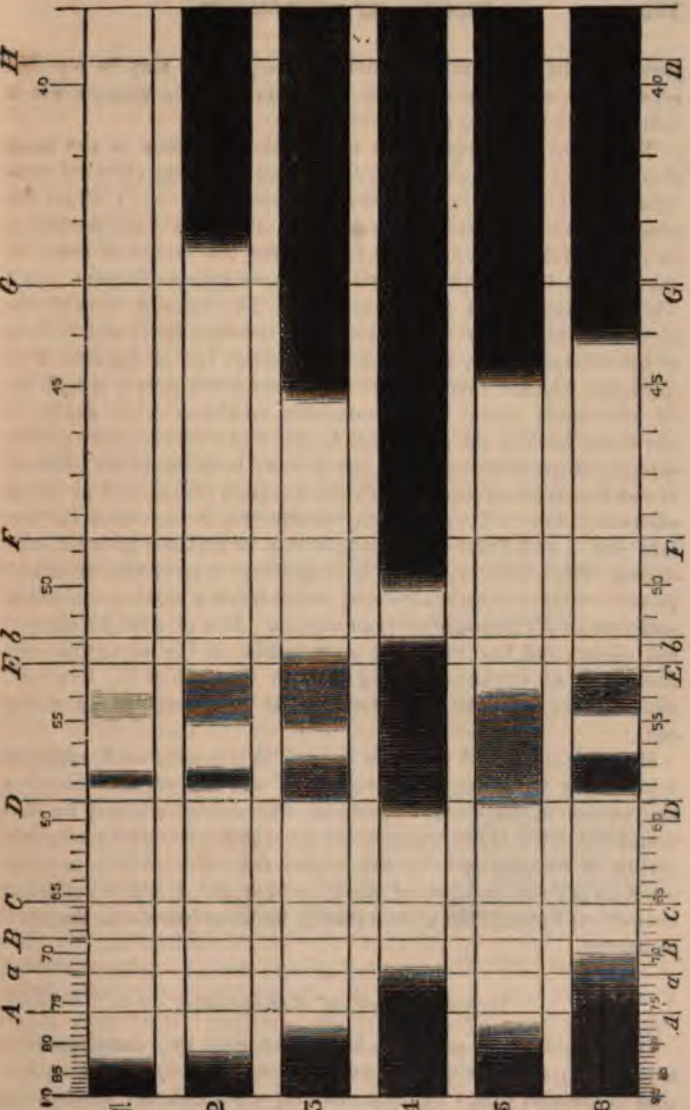


Fig. 107.—The Spectra of Oxyhæmoglobin, reduced hæmoglobin, and CO-hæmoglobin. (Gamgee.)

1, 2, 3, and 4. Oxyhæmoglobin increasing in strength or thickness of solution.
5. Reduced hæmoglobin. 6. CO-hæmoglobin.

jurious to the blood, the reduction and reoxidation may be repeated several times, the hæmoglobin going through the changes which take place in it during normal respiration.

The union of oxygen with hæmoglobin solutions is not mere absorption of the oxygen by the liquid, but a definite chemical combination. This is seen from the following facts :—(1.) When the pressure is removed the oxygen does not come away from the liquid in accordance with the law which governs the escape of absorbed gas (*vide* p. 193). (2.) The two substances give a different result when examined with the spectroscope. The reduced hæmoglobin gives one wide diffuse band, which lies between the D and E lines of the solar spectrum, and much of the violet end is cut off. This spectrum, which is characteristic of reduced hæmoglobin, is replaced by two bands when the hæmoglobin combines with oxygen—one broad band in the green near E, and a narrow one, more clearly defined, in the yellow close to the D line; both bands lie between D and E. With strong solutions the spectrum is darkened at either extremity, and the two bands become wider and tend to fuse into one. (3.) Further, the oxygen may be replaced by other substances which unite with the hæmoglobin. One of the most important of these is carbonic oxide, which forms a much more stable compound with hæmoglobin than oxygen. It is of a bright cherry-red colour, and has two absorption bands in the spectrum very like those of oxyhæmoglobin; that in the yellow is, however, removed a greater distance from the D line towards the violet end.

It is this compound which is formed in poisoning with carbonic oxide. The CO occupying the place of the oxygen, thus destroys the function of the blood corpuscles. CO-hæmoglobin may be distinguished from O-hæmoglobin by not being reduced by reagents greedy of oxygen, and by the bright red colour which appears when 10 per cent. solution of caustic soda is added, and the mixture heated. O-hæmoglobin gives a muddy brown colour under the same treatment.

DECOMPOSITION OF HÆMOGLOBIN.

Hæmoglobin may easily be broken up into two constituents—namely, (*a*) a colourless substance which is nearly related to the class of proteids called globulin, and (*b*) a blackish red amorphous material called *Hæmatin*, which contains all the iron of the hæmoglobin.

This change is brought about by whatever causes the coagulation of albumin, such as the addition of acids, strong alkalies, and heat to 70° C.

HÆMATIN, &c.

Hæmatin is a secondary product, being the result of the oxidation of a substance called hæmochromogen, which is the first outcome of the decomposition of the hæmoglobin. Hæmochromogen can only be obtained in an atmosphere of hydrogen or nitrogen, as it immediately takes up oxygen to form hæmatin. The formula $C_{68} H_{70} N_8 Fe_2 O_{10}$ has been given for hæmatin. It dissolves in weak alkaline and acid solutions, but not in water or in alcohol.

Hæmatin is readily prepared by mixing acetic acid with a strong solution of hæmoglobin, which becomes a dark brown colour. The dark hæmatin can be removed by ether. But if the acid used be strong the solution of hæmatin is found to be free from iron. This iron-free hæmatin Preyer calls *hæmatoin*. If now the acid hæmatin solution be saturated with ammonia, the iron again becomes united with the hæmatoin, forming alkali-hæmatin.

HÆMIN.

Hæmatin unites with hydrochloric acid to form a crystallizable body called *hæmin* or hydrochlorate of hæmatin (Teichmann's crystals).

If blood or dry hæmatin be mixed with a small quantity of common salt, a drop of glacial acetic acid added, and the mixture boiled, small characteristic crystals appear which have been found to be produced by the union of two atoms of hydrochloric acid with the hæmatin.

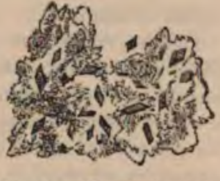


Fig. 108.—Hæmin Crystals.

The formation of these crystals is very easily accomplished with a small quantity of old dried blood; therefore this substance becomes, in medico-legal inquiries, an important test for blood stains.

Crystals of a substance called Hæmatoidin are formed in old blood-clots retained in the body. It does not contain any iron, and has the chemical formula $C_{32} H_{36} N_4 O_6$. It is probably identical with *bilirubin*, one of the colouring matters found in bile.

GLOBIN.

This name has been given by Preyer to the proteid part of the hæmoglobin, on account of its slightly differing from globulin, though it resembles it in being precipitated by the weakest acids, even carbon dioxide.

CHEMISTRY OF THE STROMA.

The stroma forms only about 10 per cent. of the solid parts of the corpuscles, the rest being hæmoglobin. The proteid basis of the stroma is probably mostly made up of a globulin, also containing lecithin, cholesterin and fats in minute proportions. There is little more than one-half per cent. of inorganic salts in the red-blood corpuscles, of which more than half consists of potassium phosphate and chloride.

DEVELOPMENT OF THE RED DISCS.

In the early days of the embryo the blood-vessels and corpuscles appear to be formed at the same time from the middle layer of the blastoderm (mesoblast). They first consist of round, nucleated, colourless cells, which subsequently become coloured, gradually lose their nucleus, and assume the characteristic shape of the red corpuscles, the rest of the original mass of protoplasm remaining as a rudimentary blood-vessel.

In the later stages of embryonic life the red corpuscles are said to be formed in the liver, possibly out of protoplasmic elements which are made in the spleen and thence carried to the liver by the portal circulation.

In the connective tissue of rapidly growing animals—tadpole (Kölliker), rabbit (Ranvier), rat (Schäfer) — certain cells can be seen to be connected in the form of a capillary network, and within the protoplasm of these cells red colouring matter is developed, and the particles of colour can soon be recognised as characteristic blood corpuscles, arranged in rows within the newly-formed networks. Thus isolated small networks of capillaries, consisting of a few meshes filled with blood corpuscles, are formed independently of the general circulation.

These corpuscles and their hæmoglobin are manufactured by isolated protoplasmic elements in the connective tissue, and subsequently added to the general mass of blood by the growth of the network bringing it into continuity with the neighbouring vessels.

In the adult the formation of red blood corpuscles is of course much less active, but certainly never ceases to take place in health, for the corpuscles must be renewed as they become worn out, and incapable of performing their function. This reproduction can go on with considerable rapidity, as we see after severe hæmorrhage, when the normal richness in hæmoglobin and corpuscles is soon arrived at. Their formation is, however, probably confined to a few special organs—spleen, liver, red medulla of bones—where transitional forms are found in such numbers as to point to the probability of the red corpuscles being the offspring of the colourless cells, whose protoplasm either manufactures anew or collects the necessary hæmoglobin, and then loses its nucleus and ordinary cellular characters.

We can only guess at the fate of the discs, but there are many things which point to the spleen as the organ in which they are destroyed. In the spleen an enormous number of protoplasmic elements are produced, and the blood comes into relationship with the nascent cells in a way unknown in any other part of the body. Further, various unusual elements, some like altered red corpuscles, others like white cells enveloping hæmoglobin, are found in this organ.

The blood corpuscles on coming to the spleen are possibly submitted to a kind of preliminary test of general fitness, some elements of the spleen pulp having the faculty of examining their condition and deciding upon their fate. Many, no doubt, pass the trial without any change, being found in good working order. Others that are found totally unfit are broken up, and their effete hæmoglobin carried to the liver to be eliminated as bile pigment. Some possibly undergo a form of repair, a white cell taking charge of a weakly disc renews its stroma, adds to its hæmoglobin, and carries it through the final proof in the liver, where it is chemically refreshed before going to the lungs for the load of oxygen which it has to carry to the systemic capillaries.

THE GASES OF THE BLOOD.

These are present in two conditions: *i.e.* (1) dissolved in it in accordance with well-established physical laws,* and (2) chemically combined. But since the latter are but loosely combined they may be separated by the same means as the former, and thus the oxygen, carbon dioxide, and nitrogen can all be removed by reducing the pressure with the air-pump. For this purpose a mercurial pump must be used, by means of which a practically perfect vacuum can be formed and all the gases obtained in a manner which facilitates further analysis. Together they are found to measure about 60 volumes for every 100 volumes of blood.

---

* I. A given liquid absorbs the same *volume* of a given gas independent of the pressure exercised by that gas.

II. At the same temperature the volume of a gas varies inversely with the pressure, so that with twice the pressure a given volume of a gas is twice the weight.

III. Therefore the amount *by weight* of gas absorbed by a liquid depends directly on the pressure, being *nil* in vacuo.

The weight of a given volume of a gas decreases as the temperature increases, therefore the amount of gas absorbed is in inverse proportion to the temperature being practically *nil* at boiling point.

Oxygen.—The amount of oxygen in the blood is found to vary much with circumstances. In arterial blood the quantity is much more constant, and always exceeds that in venous blood. It is estimated (at 0° C. and 760 mm. pressure) that every 100 volumes of arterial blood yield 20 volumes of oxygen, whilst the volume of of oxygen in venous blood varies from 8 to 12 per cent.

The oxygen which comes off in the Torricellian vacuum exists in the blood in two distinct states:—(1) a very small quantity simply absorbed,—about as much as water absorbs under atmospheric pressure; (2) chemically combined, in which state nearly all the oxygen exists, and forms with the hæmoglobin a loose combination called oxyhæmoglobin. This oxygen therefore does not follow the laws of absorption by leaving the blood in proportion as the pressure is reduced, but at a certain point of reduction of pressure (20 mm. mercury) the oxygen comes off almost completely.

Carbon Dioxide (CO_2).—The amount of carbon dioxide also varies more in venous than in arterial blood, for under certain circumstances (suffocation) it may rise to over 60 volumes per cent., although ordinary venous blood on an average contains only 46 volumes in every 100. On the other hand, the amount of this gas in arterial blood varies little from 39 volumes per cent.

The larger proportion of carbon dioxide exists in the plasma, where it appears to be chemically combined with soda salts.

Nitrogen.—The amount of nitrogen does not vary much, being in both venous and arterial blood about 1·5 volume per cent., and it would appear to be simply absorbed.

For further details about arterial and venous blood, *see* Respiration.

CHAPTER XV.

COAGULATION OF THE BLOOD.

IN speaking of the chemical relationship of the plasma (see p. 173), the formation of fibrin has been mentioned as the essential item in coagulation, and the relation of fibrin to its probable precursors has been discussed. If the points there explained be borne in mind, and the presence of the corpuscles be taken into account, the various characteristics of the clot which forms when blood is shed into a vessel can be easily understood, and should require no further description. The great importance of the coagulation of the blood in pathological processes makes it expedient, however, to consider more closely the steps of the process as well as the various circumstances under which it occurs after its removal, as well as in the living vessels.

Before the formation of a perfect clot, blood may be seen after it is shed to pass through three stages: 1, viscous; 2, gelatinous; 3, contraction of clot and separation of serum.

The first stage is very short and in thin layers of blood passes immediately into the second. With considerable quantities of blood, contained in deep vessels the central parts take some little time to turn into a firm jelly, so that the completion of the second stage may occupy from one to thirty minutes.

After from ten to fifteen hours the third stage begins; clear drops of serum appear about the clot which contracts until it forms but a comparatively small mass floating in the serum. If the jelly-like clot be disturbed, the serous fluid makes its appearance much sooner than the time just stated.

During the formation of the clot under ordinary circumstances the corpuscles are entangled in the meshwork of fibrin, so that the gelatinous mass has throughout a dark red colour.

If the coagulation takes place slowly—as it does in very cold weather, in horses' blood, or in human blood if removed from a person during fever—then the heavier red corpuscles have time to subside to the lower layers of the clotting plasma, while the white cells are caught in the meshes of the fibrin and remain in the upper layer of the clot, which then has the pale colour familiar to the physician in the old days of bleeding as the "buffy coat," or *crusta phlogistica.* This buffy coat contains a greater proportion of the elastic fibrin and soft white cells than the rest of the clot, and encloses but few red corpuscles, therefore the fibrin can contract more completely in this upper layer than in the deeper part of the clot, which includes the red corpuscles. The effect of this is, that the upper surface becomes concave, and a "cupped" clot is formed. The contraction of the clot proceeds for days, and in order to see the characters described above the blood should be kept in a cool place and perfectly motionless.

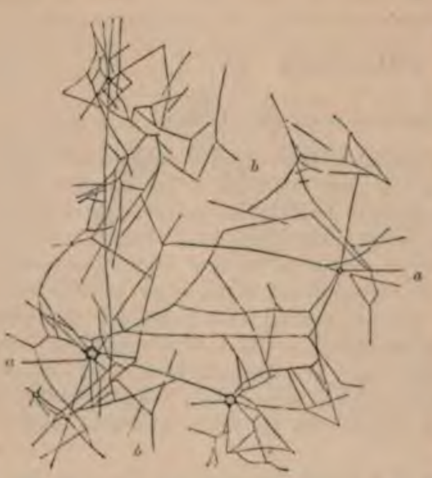


Fig. 109.—Reticulum of Fibrin Threads after staining has made them visible. The network (*b*) appears to start from granular centres (*a*). (Ranvier.)

The contraction of the fibrin and separation of the serum can be made to take place much more quickly by gentle agitation causing the ends of the fibrin threads to separate from the sides of the vessel, but by thus disturbing the clot, during its formation, the corpuscles are displaced and escape into the serum, which is thus stained and cannot be seen in its clear transparent state.

If brisk agitation with a glass rod—or better, a bundle of twigs—be commenced the moment the blood is drawn, the fibrin is formed more rapidly, but the corpuscles are not entangled in its meshes, for as quickly as the elastic threads are formed they adhere firmly to the rod or twigs. Thus the fibrin is formed very rapidly, and the ordinary blood-clot, consisting of fibrin and the corpuscles, does not appear, for the fibrin is separated from the latter during the coagulation. We then have what is commonly spoken of as "defibrinated blood," which does not give a clot. Not that the clotting has been prevented, but the material essential for the formation of a clot has been removed as quickly as formed, and instead of catching the corpuscles in the meshes of its delicate fibrils to form the clot in the ordinary way, the stringy shreds of fibrin cling around the beating-rod as a jagged mass. The following tables show the relation of the different constituents of coagulated and defibrinated blood respectively :—

$$\text{Living Blood} = \left\{\begin{array}{l}\text{Plasma}\\ \text{Corpuscles}\end{array}\right\} = \left\{\begin{array}{l}\text{Serum (appearing as clear fluid).}\\ \left.\begin{array}{l}\text{Fibrin}\\ \text{Corpuscles}\end{array}\right\} = \text{Blood clot.}\end{array}\right.$$

$$\text{Living Blood} = \left\{\begin{array}{l}\text{Plasma}\\ \text{Corpuscles}\end{array}\right\} = \left\{\begin{array}{l}\text{Fibrin (removed on the rod).}\\ \left.\begin{array}{l}\text{Serum}\\ \text{Corpuscles}\end{array}\right\} = \begin{array}{c}\text{Defibrinated}\\ \text{blood.}\end{array}\end{array}\right.$$

Many circumstances influence the rapidity with which a blood clot is formed. Speaking generally, the removal of the blood from its normal supply of nutrition and from the opportunity of preserving the necessary equilibrium of chemical interchange between the corpuscles, the plasma, and the tissues—in short, circumstances which tend to injure the corpuscles or the plasma, and promote the changes resulting in their death—must hasten coagulation ; while, on the other hand, the conditions which protect the corpuscles and impede the stages in fibrin formation must retard coagulation.

These may be arranged categorically, viz.

A. Circumstances promoting coagulation :—

1. *Contact with foreign bodies* is of the first importance in hastening coagulation. The greater the surface of contact with the vessel or the air, the more the corpuscles are exposed to injury, and the more rapid are the destructive chemical changes inducing fibrin formation. Thus a drop or two of blood falling on any surface so as to spread out in a thin layer clots almost instantly.
2. *Motion*, by renewing the points of contact between the blood and the moving agent hastens coagulation. Thus, by whipping fresh blood, all the fibrin can be removed in a few minutes, and the defibrinated blood left without a clot.
3. *Moderate heat.* The formation of the fibrin generators and the action of the ferment seem to go on more rapidly at 38°—40° C. than any other temperature.

4. *A watery condition of the blood* causes rapid coagulation but a soft clot. This is seen in repeated bleedings or hæmorrhages; the blood which flows last clots first.
5. The addition of *a small quantity* of water by setting up rapid changes in the corpuscles accelerates coagulation.
6. *A supply of oxygen.*—Oxygen is used up in the chemical changes attendant upon the death of the blood, and its presence aids the formation of firm clots, such as are produced in arterial blood. Exposure to the air in a shallow vessel facilitates coagulation, partly by extensive contact and partly by a free supply of oxygen. But exposure to air is not necessary, for blood collected in mercury, without ever coming in contact with the air, coagulates very rapidly.

B. Circumstances which retard coagulation:—

1. Constantly renewed and close inter-relationship with the *lining of healthy blood-vessels* alone affords the requirements essential for the preservation of the living corpuscles and plasma in their normal condition.
2. When the blood is surrounded by *healthy living tissues* interchanges may occur between them, and if the oxygen supply is deficient, coagulation is much delayed. Thus considerable quantities of blood effused into the tissues may be liquid and black for many days after its escape from the vessels. This dark blood clots on removal and exposure to the air.
3. *Low temperature.*—The rate of coagulation decreases with a temperture below 38° C., and the process is checked at 0° C.
4. *A great quantity* of water seems to render the action of the fibrin factors weak.
5. The addition of *egg albumin*, *syrup* or *glycerine*, retards the process.
6. The addition of concentrated solutions of neutral salts (about three volumes of 30 per cent. solution of magnesium sulphate) quite prevents coagulation.
7. The addition of small quantities of alkalies.
8. The addition of acetic acid until very slight acid reaction is obtained.
9. Increase in the amount of carbon dioxide. This, together with the want of oxygen, explains why vencus blood clots more slowly and loosely than arterial, and why the blood in the listended right side of the heart is commonly liquid *after* death from suffocation.

10. The blood of persons suffering from inflammatory disease coagulates slowly, but forms a very firm clot.

Since the blood coagulates spontaneously when removed from the body, the question now arises, how does it remain fluid in the blood-vessels?

Though this question has long occupied much attention, it is still difficult to formulate a definite answer. Nor can we expect to find any adequate explanation until we are better acquainted with the exact details of the origin of the fibrin generators. It must be remembered that the blood should be regarded as a tissue, made up of living constituents requiring constant assimilation and elimination for the maintenance of its perfectly normal conditions and life. One can confidently say that coagulation is the outcome of certain chemical changes concomitant with the death of this tissue, and that while the tissue lives no such changes take place. But such an answer adds little to our knowledge of the matter.

Since constant chemical intercourse must be kept up between the blood and its surroundings in order to sustain the complex chemical integrity essential for its life, we cannot be surprised that its waste materials accumulate, and that it soon dies when shed, just as other tissues do when deprived of their means of support. The formation of a solid and the separation of a liquid form of proteid is in no way unusual as a first step in the decline from exalted chemical construction, for similar changes occur in other tissues, and in protoplasm itself. The soft contractile substance of muscle, probably during its contraction, and certainly at its death, tends to undergo almost exactly the same kind of change as the blood in coagulation.

If we knew accurately the nutritive process taking place in the blood itself, and with which of its surroundings it keeps up chemical interchange, the answer would be much simplified. But we have in the blood three elements that probably have different modes of assimilation and elimination, viz., plasma, white cells, and red discs. But we practically know nothing of the changes they undergo during their nutrition; or whether their tissue changes have any necessary relation to those of the neighbouring tissues. We do know, however, that there exists some very intimate relation between the membrane lining the vessel walls and the contained blood. They seem to require frequently repeated contact one with the other in order that the normal condition of both may be maintained in perfect, vital, integrity. Thus fresh supplies of blood are required by the vessel wall, for when deprived of its nutriment by a stoppage of the blood-flow, it soon loses its power of retaining the blood, and admits of extravasation; and renewed contact with the vessel wall is equally necessary for the blood, for the cells congregate, and the plasma, when the stasis becomes injurious to the intima, coagulates. Probably the chemical changes going on in the one are useful for the nutrition of the other, and that they mutually supply one another with some material essential for their life. This is apparent in those cases where coagulation takes place during life in the vessels. It never occurs so long as the intima of the vessel is perfect, and the blood-flow constant, but it follows lesion of this delicate membrane, whether caused by injury or by mal-nutrition.

The gradual occurrence of this impairment of function of the intima can be watched under the microscope in the small vessels of a transparent part during the initial stages of inflammation. Owing to the arrest of the flow of blood, the walls of the small vessels suffer from defective nutrition, and may be seen to allow some elements to escape, while the discs adhere together and the blood coagulates.

In the larger vessels the same thing occurs when inflammation of their lining membrane destroys its capability of keeping up the necessary nutritive equilibrium. Thus clots form on the inner lining to the walls of an inflamed vein, often growing so as to fill the entire vessel, and give rise to a condition called *thrombosis.*

On the left valves of the heart and in the arteries, where the delicate intima is subjected to great mechanical strain, it is common enough to find slight injuries of it covered over with thin clots. To the surgeon this mutual nutrition of intima and blood is of the utmost importance in studying the occlusion of vessels, for it is upon this fact he has mainly to depend for the stoppage of hæmorrhage from a wounded artery. A tightly-tied ligature either injures the inner coats mechanically, or starves the intima by checking the flow of blood through the vessel up to the next branch, and that portion of the vessel is filled with stationary blood, which soon clots and forms an adherent plug. But if the ligature be applied too loosely, a slight blood current passes through the point where the vessel is tied, and this suffices for the nutrition of the intima by the renewal of the blood's contact, so that no clot is formed, the vessel is not closed, and most probably when the ligature has cut through the outer coat, secondary hæmorrhage occurs.

It has also been shown that if any foreign substance, such as a thread, be introduced into the blood while circulating, a coagulum will form around it. From this it would appear that the presence of a substance which cannot carry on the necessary chemical intercourse with the blood will excite irritation in its elements, and so effect slight local death of the plasma and the production of fibrin.

The time required for the production of intravascular coagulation as a result of mere stasis is happily long, for it has been found that the blood current may be stopped in a limb, by pressure or otherwise, for many hours without coagulation occurring. Indeed, cases have occurred where a tight bandage has stopped the circulation for an entire day without coagulation taking place. This is explained by the fact that so long as the intima lives, the blood remains fluid; in short, the tissues die before the blood clots in the vessels.

The tissues continue to live for some time after an animal is dead, and so we see the blood remains fluid in the vessels a long time after death; in fact, as long as the vessel wall can nourish itself and live. Thus it has been shown that the blood in a horse's jugular vein separated by ligature from the circulation, and removed from the animal, will remain fluid for fully twenty-four hours.

In cold-blooded animals the tissues live for even a longer time. The heart of the tortoise, if kept under suitable conditions, will beat for two days when removed from the body, and, as Brücke has shown, blood contained in it will remain fluid until after the heart is dead.

If the details of fibrin formation be followed within the blood-vessels, it is found that the injured spot or foreign body first becomes covered over with white corpuscles, around which threads of fibrin appear attached to the rough surface. As more fibrin is formed and the layer thickens, only a few cells can be seen in its meshes, but a great number always exist on the surface of the new fibrin, forming a layer between it and the blood. It is, moreover, remarked that coagulation has some relation to the abundance of white cells in all spontaneously coagulating fluids. The more cells, the firmer the clot. In pathological exudations also, and those acute serous collections which coagulate on removal from the body, fine granular threads of fibrin seem to start from the white cells, and radiate from them in a stellate manner.

Alex. Schmidt believes that a great number of white blood cells undergo chemical disintegration the instant the blood is shed, and he considers that the fibrin ferment, and probably other fibrin generators, are the result of the destruction of these weak cells; and he excludes the red corpuscles from taking any share in the process.

However, there is good evidence that the plasma and the discs can give rise to all the fibrin factors, and we know that in the circulation white cells must be destroyed and yet cause no coagulation.

Moreover, if some blood be allowed to flow into a fine capillary tube, the white cells can be seen to move away from the red discs, and the formation of the clot—a delicate fibrin network enclosing the discs—may be watched. Here the white cells exhibit manifestations of life for a considerable time after the clot has been formed, and their death could not have been the source of the fibrin factors.

In conclusion, then, we can only suppose that as in other tissues some chemical changes must go on in the elements of the blood. These changes give rise to new products which may produce fibrin, and hence cause coagulation. But so long as the elements of the blood are frequently brought into close relationship with a healthy vessel wall, the fibrin factors are either produced in such small quantity as to be ineffectual, or they are altered, destroyed, or taken up by the intima and possibly utilised for its nutrition. When the blood is removed from the vessels, the production of the fibrin factors proceeds effectually, either on account of the blood elements undergoing destructive changes, and accumulating the products—fibrin generators; or owing to the impossibility of re-integration, the fibrin factors suddenly appear as a product of lethal chemical change or decomposition.

In accepting the first view, we only adopt the theory of John Hunter, who thought coagulation was an act of life. If we adopt the other view, we must needs say it is an act of death. But, after all, this is a mere difference in degree, for how can we distinguish between the failure of a tissue to re-integrate or repair its normal chemical changes upon which its life depends, and the inevitable result of this failure (if prolonged beyond a certain point) namely, its death?

When white cells congregate at a point from which the intima is stripped from a vessel, their more active exertion possibly produces more ferment, &c., and at the same time they remain at the injured part of the vessel wall, and the removal of the fibrin factors cannot occur, since the intima is destroyed; hence, local clots are formed which extend over the injured surface, and by a process of organisation, probably the repair of the denuded patch can be accomplished.

CHAPTER XVI.

THE HEART.

The course taken by the blood on its way to the various parts of the body is called the circulation, on account of its having to make repeatedly the circuit of vessels leading from and to the heart. The heart is the great motor power which drives the blood through all the vessels, of which there is one set leading from and to the organs of the system generally, and another set leading to and from the lungs.

Anatomists speak of two circulations—the greater or systemic, and the lesser or pulmonary. However, if we follow the course of the blood, we see that both these sets of vessels really belong to the one circulation, and in fact form but one circuit. The blood passing through the lungs and systemic vessels consecutively visits the heart twice on its way, in order to acquire the force necessary to overcome the resistance of the two sets of capillaries. Although in all the higher animals the heart forms but a single organ, it practically is composed of two muscular pumps which are anatomically united but distinct in function. In its course round the circulation the blood visits each of these functionally distinct hearts at quite different parts of its circuit. The right heart is placed before the pulmonary vessels and pumps the blood through the lungs. The left heart is placed before the systemic vessels and pumps the blood through the body generally. Thus anatomically there appear to be two circulations and but one heart; physiologically there is one circulation and two hearts; or two points of resistance and two distinct pumping organs to drive the blood through the obstacles.

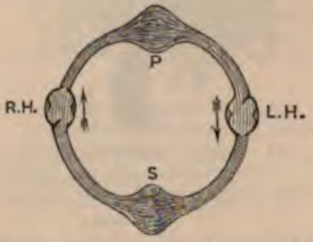


Fig. 110.—Diagram of Circulation, showing right (R.H.) and left (L.H.) hearts, and the pulmonary (P) and systemic (S) sets of capillaries.

The circulation might then be represented by a simple diagram (Fig. 110) in which the direction of the current is indicated by the arrows. L. H. shows the position of the left or systemic pump, and S. the resistance in the systemic vessels. R. H. represents the pulmonary pump and P. the second obstacle in the circuit, viz., the vessels of the lungs.

However, it must be remembered that the right and left pumping organs are fused into one viscus, which has two distinct and separate channels for the passage of the blood through it. In each system of blood vessels we have the same general arrangement for the distribution and re-collection of the blood.

In passing from either the right or left side of the heart the blood flows into tubes called arteries, which divide and subdivide until the branches become microscopical in size. From the very minute arteries the blood passes into the capillaries, which cannot be said to branch but are arranged so as to form a network of delicate tubes with more or less close meshes, according to the part.

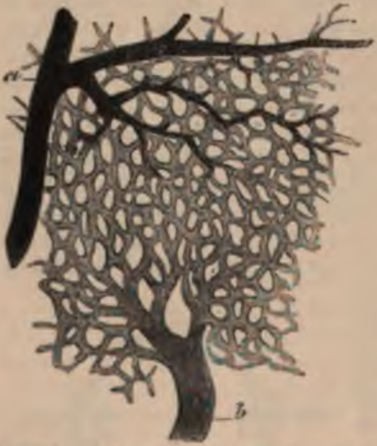


Fig. 111.—Capillary Network of the Choroid of a Child of a few months old. (Cadiat.)

(*a*) Artery. (*b*) Vein, and capillary network intervening.

Connected with the meshes of the capillaries are other small vessels which collect the blood from the networks (fig. 111). These unite one with another to form larger vessels which again are but the tributaries of the larger veins which bear the blood back to the heart.

About three hundred years ago the true course of the blood current through the systemic and pulmonary heart, arteries and veins, so as to form one circle, was demonstrated by Harvey. Before his time only the so-called "lesser" or pulmonary circuit was known. But the magnifying glasses at his disposal did not enable him to see the capillaries which were first described by Malpighi some fifty years later.

In the hope of making the general differences of functions more striking, the various parts of the circulatory apparatus may be enumerated according to their several duties and roughly illustrated by a diagram :—

1. The left (systemic) heart (L. H.) pumps the blood into the *systemic arteries,* and thus keep these vessels over-filled.

2. The larger systemic arteries (A.), by their elasticity exert continuous pressure on the blood with which they are distended.

3. The smaller systemic arterioles (A′.), by their vital contractility, check and regulate the amount of blood flowing out of the larger arteries into the capillaries, and thus keep up the tension of the larger arteries.

4. The systemic capillaries (S. C.), where the essential operation of the blood is carried out, viz., the interchange between it and the tissues.

5. The wide systemic veins (V.), are the passive channels conveying the impure blood to the pulmonary heart.

6. The right (pulmonary) heart (R. H.), pumps the blood into the pulmonary arteries and over-fills them.

7. The pulmonary arteries (P.A.), press steadily upon the blood and force it through the following, viz.,

8. Small pulmonary arterioles (P.*a*.), which regulate the flow into the capillaries.

9. The pulmonary capillaries (P. C.), where the blood is exposed to the air, and undergoes active gas-interchange.

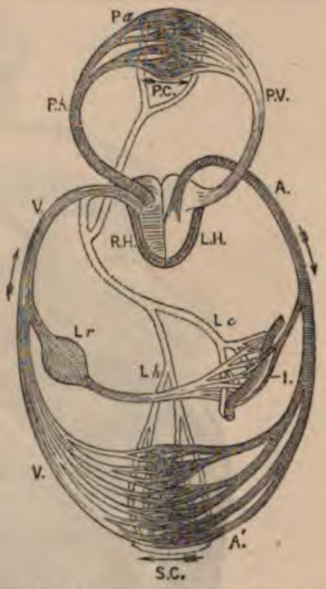


Fig. 112.—Diagram of the Circulation of the Blood and the absorbent vessels. For details see text.

10. The pulmonary veins (P. V.), carrying the blood to the left heart, and thus completing the circuit.

Lh. indicates the lymphatics, which drain the tissues, and Lc. the lacteals, which absorb from the stomach and intestines (I).

Although the blood enters the arteries by jerks, the motion through the capillaries is constant. The reason of this is, that the arteries are constantly overfull, their elastic walls being distended by the pumping of the heart, which fills the aorta and arteries more quickly than they can empty themselves, until the adequate pressure is attained through the contracting arterioles. The arterioles are the chief agents in resisting the outflow, and keeping up the arterial pressure.

THE HEART.

The heart of man and other warm-blooded animals may be said to be made up of two muscular sacs, the pulmonary and systemic hearts, or, as they are commonly termed, the right and left sides of the heart, between which no communication exists in the adult. Each of these

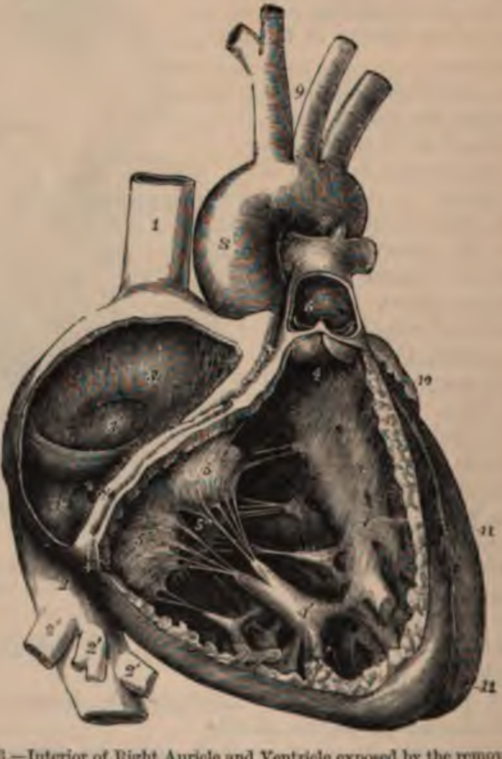


Fig. 113.—Interior of Right Auricle and Ventricle exposed by the removal of a part of their walls. (Allen Thomson.)

1. Superior vena cava.
2. Inferior vena cava.
2'. Hepatic veins.
3, 3', 3''. Inner wall of right auricle.
4, 4. Cavity of right ventricle.
4'. Papillary muscle.
5, 5', 5''. Flaps of tricuspid valve.
6. Pulmonary artery, in the wall of which a window has been cut.
7. Placed on aorta is near the ductus arteriosus.

sacs may be divided into two portions: the one, a kind of antechamber, which receives the blood from the veins, is called the *auricle*, and has very thin walls; the other, the *ventricle*, is the powerful muscular chamber which pumps the blood into the aorta and distends the arteries. (See figs. 113 and 114.)

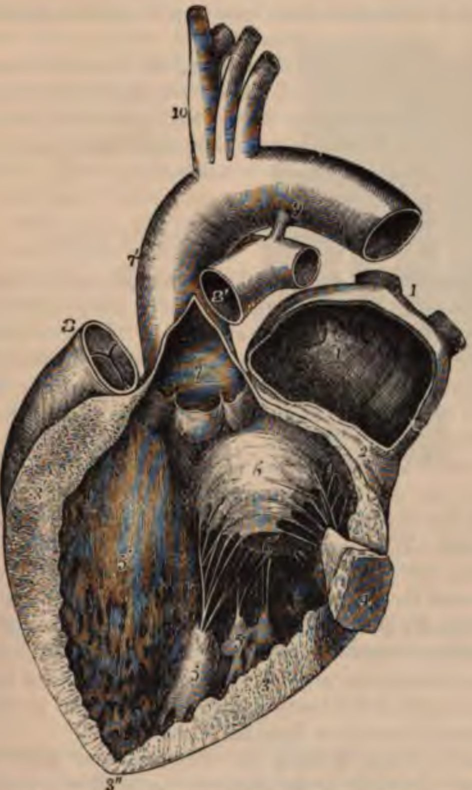


Fig. 114.—The left Auricle and Ventricle opened and part of their walls removed to show their cavities. (Allen Thomson.)

1. Right pulmonary vein cut short.
1'. Cavity of left auricle.
3. Thick wall of left ventricle.
4. Portion of the same with papillary muscle attached.
5, 5'. The other papillary muscles.
6. One segment of the mitral valve.
7. In aorta is placed over the semilunar valves.

In the empty heart the great mass of the organ, which forms a blunted cone, is made up of the ventricles, while the flaccid auricles are found retracted to an insignificant size at its base. The four cavities have about the same capacity, namely, about six ounces or eight cubic inches when distended.

The walls of both the auricles are about the same thickness, while the amount of muscle in the wall of the ventricle differs materially on the two sides. The wall of the left ventricle, including that part which forms the interventricular septum, is nearly three times as thick as that of the right or pulmonary ventricle.

ARRANGEMENT OF MUSCLE FIBRES.

At the attachment of each auricle to its corresponding ventricle there is situated a dense ring of tough connective tissue, which surrounds the openings leading from the auricles to the ventricles. Similar tendinous rings (zona tendinosa) exist around the orifice of the aorta and pulmonary arteries. These tendinous rings form the basis of attachment for the muscle bundles of the walls of both the ventricles and auricles.

In the ventricles many layers of muscles can be made out. The outer fibres pass in a twisted manner from the base towards the apex, where they are tucked in so as to reach the inner surface of the ventricular cavity. They then pass back to be attached at the base; some passing into the papillary muscles are connected with the cardiac valves through the medium of the chordæ tendiniæ; and the others forming irregular masses of muscle on the inner surface of the cavity, pass in various directions towards the base, to be fused with the tendinous rings around the arterial orifices. Another set of layers passes transversely around the ventricle lying between the inner and outer sets, and passing nearly at right angles to them.

The muscle fibres forming the thin auricular walls have their origin from the zones of the auriculo-ventricular orifices, and pass very irregularly around the cavities. The outer set of fibres have a transverse, the inner a longitudinal direction. Bands of fibres encircle the orifices of the great veins, and extend for some little distance along the vessels, particularly on the pulmonary veins, which have thick circular muscular coats after they leave the lungs.

The fibres of the auricles are not directly continuous with those of the ventricles, the auricular and ventricular fibres being only related to each other by their points of origin, viz., the auriculo-ventricular fibrous zones.

MINUTE STRUCTURE.

The muscle tissue of the heart differs both in structure and mode of action from the other forms of contractile tissues of the body. The elements are firmly united with one another to form an irregular close network, which, however, can be broken up into masses easily recognisable as peculiar cells. These cells are irregular prismoidal blocks with blunt ends, often split into two to allow of connection with the two contiguous cells. They contain a distinct nucleus, situated in the central axis of the cell. The cells are not surrounded by a distinct sheath of sarcolemma.

Though striated, like the skeletal muscles, the action of the heart muscle is peculiarly independent of the great nervous centres, being quite involuntary, and characterised by a definite periodicity. Its contraction is very slow when compared with the skeletal muscles, but it is much more rapid than that of the contracting tissues of most of the hollow viscera.

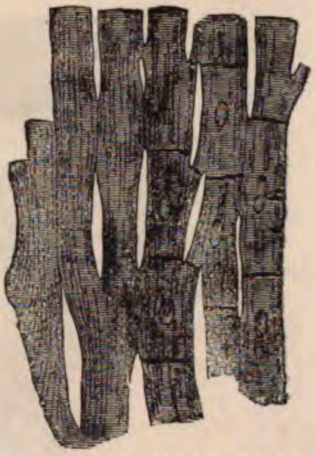


Fig. 115.—Striated Muscle Tissue of the Heart, showing the trellis-work formed by the short branching cells, with central nuclei.

VALVES.

The orifices which lead into and out of the ventricles have peculiar arrangements of their lining texture, forming valves which allow the blood to pass in a certain direction only. These valves, which form a most interesting and important part of the economy of the heart, are of two kinds, differing completely in their mode of action. One kind directs the passage of the blood from the auricles to the ventricles, the other guards the openings into the great arteries. The auriculo-ventricular openings are protected by valves with a sail-like action. These are made up of delicate curtains formed of thin sheets of connective tissue arising from the margins of the auriculo-ventricular openings, which form the fixed attachment cf each of the curtains of the valves. The free edges and ventricular surfaces of the curtains are blended with the tendinous cords coming from the papillary muscles, and thus give points of tendinous attachment to some of the bundles of muscle fibres in the wall of the ventricle. At the right auriculo-ventricular opening there are three chief curtains; hence it is called the "tricuspid" valve (Fig. 117, RAV). The opening from the left auricle to the left ventricle, which is about one-third smaller, is guarded by two large valvular flaps, and is hence called the "bicuspid," or more commonly "mitral" valve (Fig. 116). The arterial valves are made up of three deep pockets with free semilunar margins looking towards the vessel. The curved base of each pocket is attached to the arterial orifice of the ventricle, with the lining membrane of which it is continuous.

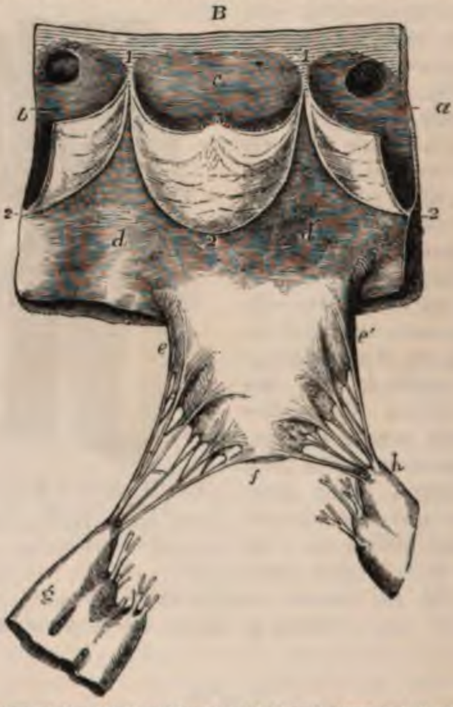


Fig. 116.—Portion of the Wall of Ventricle (*d d′*) and Aorta (*a b c*), showing attachments of one flap of mitral and the aortic valves; (*h* and *g*) papillary muscles; (*e*, *e′*, and *f*) attachment of the tendinous cords. (Allen Thomson.)

ACTION OF THE VALVES.

The mode of action of the flaps of the tricuspid and mitral valves is like that of a lateen sail of a boat, if we substitute the blood stream for the air current; the tendinous cords acting as the "sheet" or rope which restrains the sail when filled with wind.

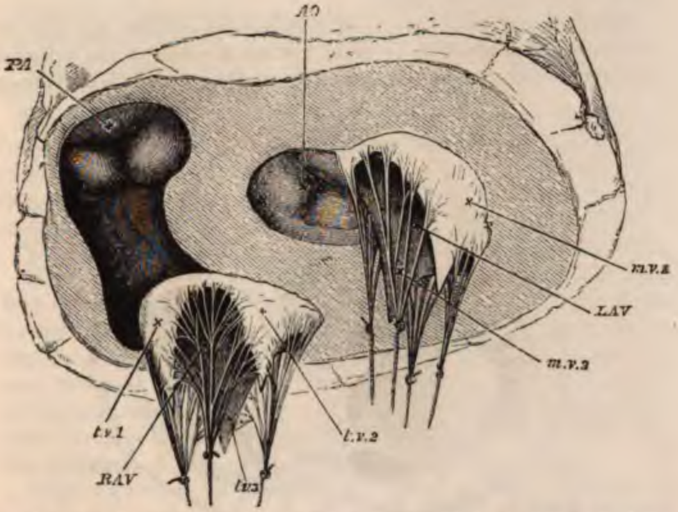


Fig. 117.—The Orifices of the Heart seen from below, the whole of the ventricles being cut away, and the curtains of the auriculo-ventricular valves drawn down by threads attached to the chordæ tendinæ. (Huxley.)

RAV. Right auriculo-ventricular opening surrounded by the flaps of tricuspid.
LAV. Left auriculo-ventricular opening and attached mitral valve.
PA. Pulmonary valves when closed. *AO*. Aortic valves closed.

The blood driven in from the auricle at first pushes the curtains of the valves against the ventricular wall, and immediately fills the ventricle. As the ventricle becomes distended the tendinous cords coming from the elastic papillary muscles are put on the stretch, and draw the valve curtains away from the wall of the ventricle into the midst of the fluid. When the ventricle begins to contract upon its contained blood, the pressure of the fluid bellies out the sail-like valves towards the auricles, so that their convex sides come into close apposition with one another. Their free margins are held firmly by the papillary muscles contracting and tightening the cords. The flaps are kept at much the same tension by the papillary muscles shortening in proportion as the ventricle empties itself and the cavity diminishes in size. By this mechanism the valves are prevented from bulging too much into the auricles, or allowing the blood to pass back into them.

The semilunar valves are mere membranous pockets, and have no tendinous cords attached to them, but on account of the extent of their curved attachment, when their limited free margin is made tense by the pocket being filled from the artery, the valves can only pass a given distance from the wall of the vessel and are thus held firmly in position. When the force of the blood leaving the ventricle begins to diminish, the semilunar flaps are raised from the distending wall of the artery; and the moment the current from the ventricle has ceased to flow, the pockets are forcibly distended by the aortic blood pressure and bulge into the lumen of the vessel, so that the convex surface of the lunated portions of each valve is pressed against corresponding parts of its neighbour. Their union then, which is accomplished by their overlapping to some extent, forms three straight radiating lines, and is a perfectly impervious barrier to any backward flow of blood (Fig. 118, PA. and AO.).

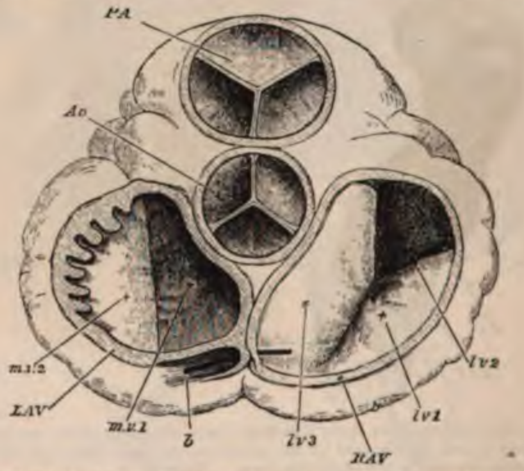


Fig. 118.—The Orifices of the Heart seen from above, both the auricles and the great vessels being removed. (Huxley.)

PA. Pulmonary artery and its semilunar valves. *Ao.* Aorta and its valves. *RAV.* Tricuspid, and *LAV.* Biscuspid valves.

MOVEMENTS OF THE HEART.

It is only by means of these valvular arrangements that the heart is enabled to perform its function, namely, to pump the blood in a constant direction onwards, emptying the veins and filling the arteries against great opposition on the part of the latter vessels.

This pumping is carried on by the successive contractions and relaxations of the muscular walls of the various cavities.

The blood, flowing from the systemic and pulmonary veins, passes unopposed into the right and left auricles respectively. As soon as the auricles are full their walls suddenly contract and press the blood into the right and left ventricles; immediately the ventricles contract, and, pressing upon the blood, force it into the great arteries.

The contraction of each pair of cavities is followed by their relaxation.

The blood cannot pass back into the veins from the auricles when they contract, because the auricular contraction commences in the bundles of muscle which surround the orifices of the great venous trunks; and it cannot flow back to the auricles, because, as has been seen, the force of the blood current on its entry into the ventricles, by making tense the cords, closes the valves; while a backward flow from the large arteries is at once prevented by the current distending the semilunar pockets, and thus firmly closing the valves.

When viewed for the first time, the beat of the heart appears to be a single act, so rapidly does the ventricular follow the auricular beat. More careful examination shows that this single action is composed of different phases of activity and repose, which together make up the cycle of the heart beat. The time occupied by the contraction of the cavities of the heart is called their *systole*, their period of rest is called *diastole*.

The systole of the corresponding cavities of both sides of the heart is exactly synchronous; that is to say, the two auricles contract simultaneously, and immediately the contraction of the two ventricles follows like that of the two auricles as a single act.

The auricular and ventricular contractions are separated by so short a space of time that it is not easily appreciable. The rapidly succeeding acts of auricular and ventricular systole are followed by a period during which both auricles and ventricles are in diastole, which is commonly spoken of as the passive interval or pause.

While the auricles are contracting the ventricles are relaxed, and the relaxation of the auricles commences immediately the ventricular contraction begins, so that only for a very short time both auricles and ventricles are contracted.

The entire cycle or revolution of the heart-beat, occupying nearly a second in the healthy adult, may be divided into three stages :—

Auricular systole.
Ventricular systole.
General diastole.

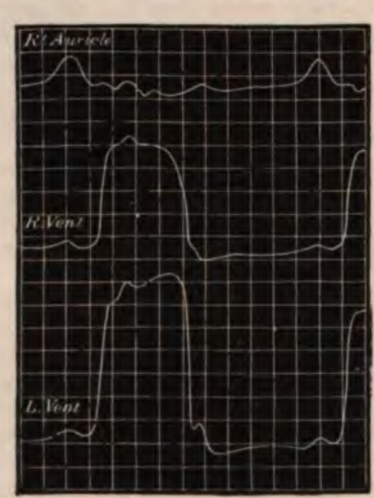


Fig. 119.—Curves drawn on a moving surface by three levers, which are connected with the interior of the heart, viz. :—

Upper line shows the changes of pressure occurring in the right auricle;
Centre line shows the pressure changes within the right ventricle;
Lower line shows the changes of pressure occurring in the left ventricle.
(The smoked surface is moved from right to left.) (After Chauvian.)

The exact time occupied by each phase of the cycle can only be calculated approximately. This may be done either by registering graphically the motions of the auricles and ventricles directly communicated to levers brought into contact with their surface, or by recording graphically the pressure changes which occur within the cavities by introducing into them little elastic sacks filled with air, whence the pressure changes are communicated to an ordinary "tambour," and registered on a smoked surface.

Of the whole period of the cycle the passive interval or pause is the longest and the most variable, for in ordinary changes in the heart's rhythm it is the pause that varies. Next in duration is the ventricular systole, while the shortest is the auricular systole.

The following figures give approximately the proportion of time occupied by each part of the cycle in the case of a horse, whose intracardiac tension was registered in the manner just referred to, while his heart beat about fifty times in the minute :—

	Proportion of cycle.		Duration in seconds.
Auricular systole	$\frac{1}{6}$	=	0·2″
Ventricular systole	$\frac{2}{6}$	=	0·4″
Passive interval	$\frac{3}{6}$	=	0·6″

Or if we assume the human heart to beat some seventy times a minute, each cycle would occupy about $\frac{8}{10}$ of a second, which would be made up as follows :—

Auricular systole . . . . = $\frac{1}{10}$ of a second
Ventricular systole . . . = $\frac{3}{10}$ „
Pause . . . . . . = $\frac{4}{10}$ „

The duration of the auricular and ventricular systole varies but little except under abnormal circumstances, but the pause is constantly undergoing slight changes. In fact, the duration of the general diastole depends upon the rate of the heart beat, being less in proportion as the heart beats more quickly.

If the thorax of a recently killed frog be opened, the heart can be observed beating *in situ*, and the different acts in the cycle studied.

In mammalians, in order to see the heart in operation, it is necessary to keep up artificial respiration, during which the heart continues to beat regularly, though the thorax be opened. A careful inspection of the beating heart shows that during its cycle of action certain changes take place in the shape and relative position of its cavities. This is owing partly to the change in the amount of their blood contents and partly to the form assumed by the muscular wall when contracting.

During the passive interval the auricles are seen to swell gradually on account of the blood flowing into them from the veins : when the auricular cavities are nearly full, a contraction, commencing in the great venous trunks near the heart, passes with increasing force over the auricles and gives rise to their rapid systolic spasm. The auricles appear suddenly to diminish in size, become pale, and empty themselves into the ventricles.

As the blood is shot through the auriculo-ventricular openings and the ventricles become distended, their flaccid walls appear to be drawn over the liquid mass by the contracting auricles, just as a stocking is drawn over the foot by the hands, and their walls seem to approach towards the base of the heart. The moment the ventricles have received their full charge of blood from the auricles they contract, becoming shorter by the movement of the base towards the apex, and thicker by the elongated ventricular cone becoming rounder. The great arteries are at the same time distended with blood and elongated, their elastic walls being drawn down over the liquid wedge on its exit from the ventricle. The soft elastic tissues are thus in turn made to slide, as it were, over the incompressible fluid blood that forms the fulcrum, which the power of the muscular walls uses as a firm purchase. During the systole, when the thorax is open, the ventricles rotate slightly on their long axis, so that the left comes a little forwards, and the apex also forwards and towards the right. On the ventricular systole ceasing, the gradual refilling of the auricles begins; the ventricles become flaccid and flattened; the semilunar valves, being closed, the large arteries grasp firmly the blood, and by their steady resilient pressure force it onwards towards the distal vessels. During this pause the arteries seem to become shorter, drawing the base of the heart up again and lengthening the flaccid ventricles.

The part of the heart which changes its position most is the line between the auricles and ventricles, while the apex remains fixed in the one position, only making a very slight lateral and forward motion, which probably does not take place during life. If a needle with a light lever attached be made to enter the apex through the wall of the chest, the lever does not move in any definite direction during the systole, but simply shakes. If, on the other hand, the needle be placed in the base of the ventricles the lever moves up and down with each systole and diastole.

Heart's Impulse.

If the ventricles be gently held between the fingers during their systole, a most striking sensation is given by the sudden hardening of the muscle. The mass of the ventricles, from being quite soft and compressible during diastole, suddenly acquire a wooden hardness owing to the tightness with which the muscle grasps the fluid, and the greater firmness of the contracting tissue.

This hardening gives the sensation of a sudden enlargement in all directions. No matter on what surface the finger be placed, the heart seems to move in that direction, so as to give a slight knock or impulse. Thus, when grasped between the forefinger placed below the diaphragm and the thumb on the antero-superior aspect the impulse is equally felt by each digit.

The heart-beat communicates its motion to the chest, and this impulse can be seen over a limited area, which varies with the thinness of the individual. This cardiac *impulse*, as the stroke is called, can be best felt in the fifth intercostal space, a little to the median side of the left nipple. It is found to be synchronous with the ventricular systole. The more important item in causing the impulse is the hardening of the ventricles, while their simultaneous change in shape, from a flattened to a rounded cone, no doubt helps to make the sudden tenseness more distinctly felt through the wall of the chest.

The point at which the impulse is best felt corresponds to the anterior surface of the ventricles some distance above the apex; it is therefore erroneous to call it the "apex beat."

Moreover, the motion of the apex is so slight when the wall of the chest is removed, that its "tilting forwards" can have no share in causing the impulse: the thoracic wall being always in contact with the apex, it can only move laterally, and cannot hammer against it so as to cause a shock. The "recoil of the ventricles" caused by the blood leaving them, which some think aids in producing the impulse, obviously owes its supposed existence to the confusion of cause and effect.

The cardiac impulse is a valuable measure of the strength of the systole, and hence is of great importance to the clinical physician. It may be registered by means of an instrument called the Cardiograph. Many such instruments have been devised, most of which work on the same principle, and write a record on a moving surface with a lever attached to a tambour, to which the movements of the chest wall are transmitted from a somewhat similar drum by means of air tubes. In using this plan, so generally employed by Marey, one air tambour (fig. 120) is applied over the heart, the motions of which cause a variation in the tension of the air it contains; these variations are transmitted by a tube (*f*, fig. 121) to the other tambour(*b*), where they give rise to a motion in its flexible surface to which a delicate lever is attached at (*a*).

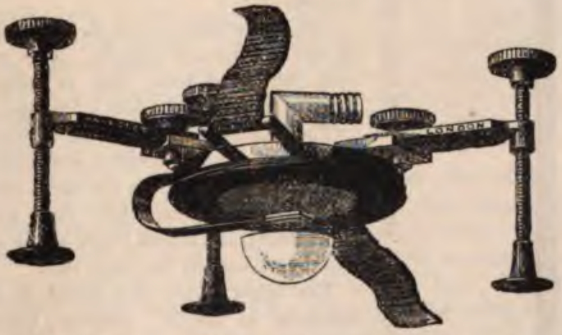


Fig. 120.—Cardiac Tambour, which can be strapped on to chest-wall, so that the central button lies over the heart-beat, and the pressure may be regulated by the screws at the side. To the tube bent at right angles is attached the rubber tube which connects the air cavity with that of the writing tambour shown in Fig. 119.

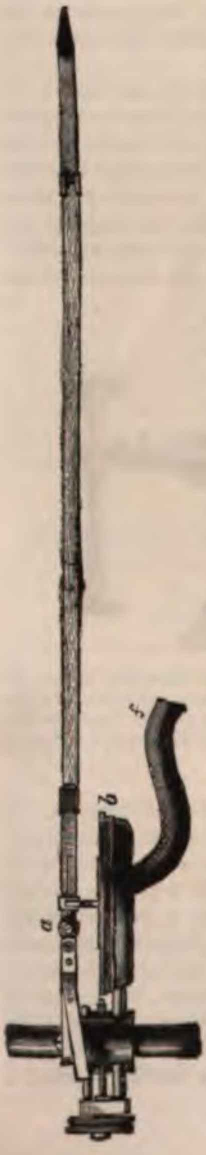


Fig. 121.—Writing Lever and Tambour. (*a*) Joint of the lever; (*b*) Air chamber; (*f*) Rubber tubing connecting it with cardiac tambour.

HEART SOUNDS.

The heart's action is accompanied by two distinct sounds, which can be heard by bringing the ear into firm direct contact with the precordial region, or indirectly by the use of the stethescope, an instrument of which there are many varieties to suit the taste of clinical observers.*

One sound follows the other quickly, and then comes a short pause; consequently they are spoken of as the *first* and *second* sounds.

The first sound occurs at the same time as the ventricular systole. It is a low, soft, prolonged tone, and is most distinctly heard over the fifth intercostal space.

The second sound is produced when the two sets of semilunar valves are closed, that is, at the moment when the blood ceases to escape from the ventricles. It is a sharp, short sound, and is best heard at the second costal cartilage on the right side.

The cause of the first sound is as yet involved in doubt. Possibly there are several factors in its production. The principal events occurring at this time may be enumerated thus:—

1. The heart's impulse.
2. The contraction of the heart-muscle.
3. The rush of blood into the arteries.
4. The sudden tension of the ventricular chambers and the auriculo-ventricular valves.

It has already been seen that the heart's impulse is caused by a sudden change in density of the muscle rather than by a knock against the chest. Moreover, the first sound is heard quite readily when the chest wall is removed, so that the apex beating against the thorax cannot even help to cause the sound.

---

* A flexible stethescope to listen to one's own heart sounds can easily be made by fitting to one end of a piece of rubber tubing about 18 inches long the mouthpiece, and to the other end the bowl, of a wooden pipe. The bowl is applied over the different regions of the heart and the mouthpiece firmly fitted in the ear.

The sound is not unlike the tone which accompanies the continuous (tetanic) contraction of the skeletal muscles. It corresponds in time and duration with the contraction of the cardiac muscle. In disease where the heart muscle is weak, the sound becomes faint or inaudible, although the valves are made tense by an intraventricular force sufficient to overcome the pressure in the arteries; for otherwise the circulation would cease. A præsystolic sound, like in character to the systolic sound, is now recognised by physicians as being produced by the auricular systole, but this cannot depend on the vibrations of valves. According to the most recent and careful observers, the first sound may be heard when the heart is empty.

All this evidence tends to show that the sound is produced by the contraction of the muscle tissue of the heart, or, in short, that it is the cardiac muscle tone.

Against the view that the muscular tone is the cause of the first sound the undoubted fact is properly urged, that only tetanus (*i.e.*, a rapidly repeated series of contractions fused into a continued state of shortening allowing variations of tension) can cause a muscle sound, and a single contraction is not accompanied by any tone. Though in many ways it differs from the single contraction of other muscles, yet the heart beat is no doubt a single contraction. And no good reason exists for believing it can cause vibrations comparable with that of the tetanus of skeletal muscles, or that it is capable of giving rise to a definite sound.

The closure of the auriculo-ventricular valves is synchronous with the beginning of the sound, and injury or disease of these valves is associated with a weak or altered first sound : this is often observed in disease of the mitral valve. The blood is said by some to be necessary for the production of the sound, so that the act of closure and subsequent tension of these valves would seem to have a share in causing the sound ; but on the other hand, the character of the sound is not like that which would be caused by the sudden closure or tension of the membranes, or of the delicate tendinous cords.

As before remarked, this would not account for præsystolic sounds, and the first sound can be heard in an empty heart removed from the animal, in which the valves could not become tense (Ludwig).

The sound has been analysed with suitable resonators, and two distinct tones made out : one high and short, corresponding to the closure of the valves; the other long and low, corresponding in duration with the muscle contraction. From this it would appear that both the tension of the valves and the muscle tone have something to do with the production of the sound.

The good reasons given for thinking that the heart muscle cannot produce a tone suggests that the sudden state of tension of the ventricular wall when tightened over the blood may give rise to vibrations, and be an important item in causing the first sound. This would explain the faintness of the sound, both when the valves were injured and the muscle weak. It would also explain the præsystolic sound, which requires a certain auricular tension for its production.

The production of the second sound is more easily explained. Occurring just after the ventricle is emptied, it is synchronous with the closure of the semilunar valves at the aorta and pulmonary orifices. The blood in the aorta forcibly closes the valves as soon as the ventricular pressure begins to wane. This sudden motion causes a vibration of the valves, which is immediately checked by the continuous pressure of the column of blood.

Innervation of the Heart.

The most interesting phenomenon in the heart's action, and that most difficult to explain, is the wonderful regularity of its rhythmical contractions under normal circumstances, and the extreme delicacy of the nervous mechanism by which it is regulated.

The vast majority of the active contractile tissues of the higher animals are under the immediate and exclusive direction of the central nervous system. All the great muscular organs are connected with the cerebro-spinal axis by means of nerves, along which impulses pass stimulating the contractile tissue to action. Thus the skeletal muscles are brought under the control of the will, and the nerves coming from the brain carry stimuli to certain sets of muscles when we wish to perform any simple action.

Other muscles, as has been seen in the pharynx, œsophagus, &c., though not under the control of the will, are yet governed altogether by the cerebrospinal axis; while others, of which the most striking example is the heart, have nerve elements in immediate relation to the contractile tissue, capable of exciting them to contraction.

It will materially help us in comprehending the nervous mechanisms of the heart's rhythm if we bear in mind what now seems to be proved beyond doubt, namely, that the muscle tissue of the heart has—quite independently of any nervous influences—an inherent *tendency* to rhythmical contraction. This is shown by the following facts. The heart cannot continue contracted like a skeletal muscle (in tetanus) under any circumstances, or like an unstriated muscle (in tonus) except when the tissue is spoiled by deficient nutrition, &c. The hearts of many of the lower animals contract rhythmically without any nerve elements being found by the most careful microscopic examination. A strip cut from the ventricle of the tortoise can, by judicious excitations, be *taught* to beat rhythmically without the help of any known nerve mechanism. The lower part of the frog's ventricle—which is commonly admitted not to contain any nerves—beats quite rhythmically if fed with a gentle stream of serum and weak salt solution, and there is no reason to assume that there is any greater difficulty in conceding to muscle tissue, than to nerve cells, the property of acting with a regular rhythm.

In cold-blooded animals, such as a frog or tortoise, the heart will beat even for days after its removal from the animal, if it be protected from injury and prevented from drying. In warm-blooded animals the tissues lose their vitality almost immediately after they are deprived of their blood supply ; however, spontaneous rhythmical movements can be seen in the mammalian heart if removed rapidly after death. The hearts of oxen, skilfully slaughtered, commonly give a few beats after their removal from the thorax. If a blood current be kept up through the vessels of the heart tissue this spontaneous contraction will go on for some time, or even will recommence after having ceased.

The hearts of two criminals who were recently hanged were found to continue to beat for four and seven minutes respectively after the spinal cord and the medulla had been separated.

These facts prove conclusively that the stimulus which causes the heart to beat rhythmically arises in the muscle tissue of the organ or in close relation to it. Upon physiological grounds alone we might conclude that in the heart tissue of the vertebrata there exist the nerve elements with which we are familiar anatomically. These nerve cells only require their nutrition to be kept up by a continued blood supply in order to develop the energy necessary for their function.

Such collections of nerve elements are called *automatic* centres, and are made up, like all other origins of nerve force, of ganglionic cells.

The heart of mammalian animals so soon ceases to beat, that it forms an unsatisfactory subject for experimental inquiry. The heart's innervation—which will be seen to be a complicated process—may, therefore, with profit be studied in a cold-blooded animal, where the mechanisms can be more readily observed, and are probably more simple in arrangement.

The frog, being readily obtainable, is commonly chosen.

If the apex of the ventricle of the frog's heart be separated, it remains motionless, while the auricles continue to beat. But it responds to short direct stimulus by an ordinary single contraction, and if the stimulus be kept up it beats rhythmically. If the auricles be removed from the ventricle so as to leave the line of union attached to the ventricle, both continue to beat. But each part beats with a

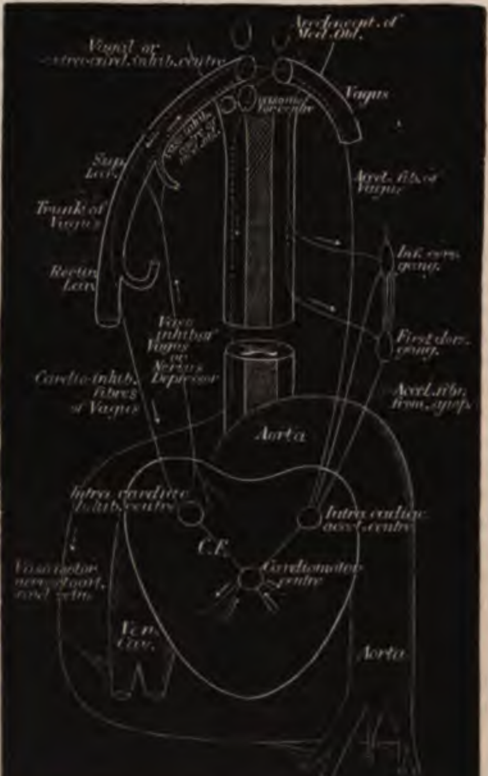


Fig. 122.—Diagrammatic Plan of the Cardiac Nerve mechanism. The direction of the impulses is indicated by the arrows. Both right and left sides of the cut are used to show one complete lateral half of the fibres.

different rhythm, and under like conditions the auricles continue to beat longer than the ventricles.

The auricles beat even when subdivided; and the dilated termination of the great vein, called the sinus venosus, opening into the right auricle, when quite separated from the rest of the heart, continues to beat longer and more regularly than any other part. When the entire heart is intact this sinus seems to be the starting point of the heart-beat.

This experimental evidence of the presence of nerve centres in the heart-muscle is supported by the results of anatomical investigations, for the microscope shows that there are many ganglion cells distributed throughout the heart-tissue, and that they are located just where we should expect from the above facts. That is to say, there are none in the substance of the ventricles, while there are several groups of cells scattered around its base in the auriculo-ventricular groove (Bidder). There are others in the walls of the auricles, particularly in the septum, and the greatest number are found in the walls of the sinus venosus (Remak).

The ganglia in the sinus venosus are most easily stimulated, and are probably the only ones which habitually act as automatic centres. They certainly take the initiative in the ordinary heart-beat, and regulate the rhythm of the contraction of the auricles and ventricles.

This seems more than probable from the following facts :—1. The ordinary contraction wave starts from the sinus venosus. 2. This part beats longer and more steadily than the others when separated from the animal. 3. When cut off from the sinus the beat of the rest of the heart becomes weak, uncertain, and changes its rhythm. 4. When the sinus venosus is suddenly separated by ligature from the auricles and ventricle, both the latter cease to beat, while the motions of the sinus continues. However, if a slight stimulus, such as the touch of a needle, be now applied to the auriculo-ventricular margin, it suffices to give rise to a series of rhythmical contractions. Or if the ventricle be now separated from the auricles by incision, the former commences to beat rhythmically, while the auricles commonly remain motionless. These latter observations (which are known as the experiments of Stannius) have been explained in various ways, the most probable of which seems to be the following. When cut off from the influence of the sinus venosus, the heart fails to contract spontaneously, because it has lost the initiatory stimulus which habitually arrived from the sinus. When the ventricle is cut away from the auricles, the act of incision is sufficient stimulus to set going its rhythmical contractions.

Although we cannot adequately explain the relationships borne by the different sets of ganglia in the frog's heart to one another, there seems no doubt that the following conclusions may be accepted as proven, and are, moreover, in all probability, applicable to the hearts of mammals :—That nerve centres exist in the muscle tissue of the heart, some of which are capable of originating stimuli for this rhythmically contracting muscle. That there exist other ganglionic groups which help to regulate and distribute the stimuli in a sequence throughout the several cavities.

EXTRINSIC CARDIAC NERVES.

The intrinsic nerve mechanism of the heart just described is under the immediate control of the great nervous centres through the medium of fibres passing along the vagus and sympathetic nerves from the medulla oblongata.

Some of these fibres check the action of the intrinsic ganglia, and cause the heart to beat more slowly ; hence they are called *inhibitory*. Others cause it to beat more quickly, and are called *acceleratory*.

INHIBITORY NERVES OF THE HEART.

It was observed by Weber that electric stimulation of the vagus nerve caused a slowing of the heart's rhythm, and if increased gave rise to a standstill of the heart in diastole ; the heart beat gradually recommencing some time after the stimulus had been removed. On the other hand, the section of both vagi produced an increase

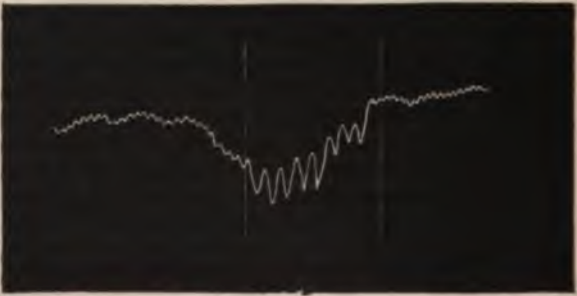


Fig. 123.—Tracing, showing the effect of Stimulation of Vagus Nerve. Stimulus applied between vertical lines. (Recording surface moved from left to right.)

in the rapidity of the heart beat varying according to the kind of animal experimented upon.

Section of only one vagus, however, has not this effect. From these experiments it would appear—1. That some fibres of the vagus bear impulses of a checking or inhibitory nature to the intrinsic nerves of the heart. 2. That these influences are constantly in operation, or in other words, the vagi exert a tonic inhibitory influence on the rapidity of the heart-beat. 3. The tonic action of one vagus bears inhibitory influence sufficient to regulate the heart's action. This tonicity of the vagus inhibition is, moreover, more marked in man and dogs than rabbits, and is reduced to a minimum in frogs, where section of the vagi produces very little effect on the rate of the beat.

Vagus inhibition is increased by the following circumstances—(*a*) certain psychical phenomena such as terror, which is said to produce a temporary standstill ; (*b*) deficiency of arterial blood in the medulla oblongata ; (*c*) increase of the blood pressure within the cranium ; and (*d*) reflexly by the stimulation of many afferent nerves, particularly the sympathetic and those bearing impulses from the abdominal viscera to the medulla, as well as the ordinary sensory nerves or by the afferent fibres of the opposite vagus. (*e*.) *Muscarine* produces diastolic standstill of the heart by exciting the local inhibitory ganglia or vagus terminals.

Atropin causes quickening of the heart's action by paralysing the endings of the vagus, and also those intrinsic mechanisms which are supposed to have an inhibitory effect. *Nicotine* produces at first a slowing of the heart by stimulating the inhibitory tone of the vagus. This is soon followed by exhaustion of the terminal fibres and a consequent quickening of the heart beat. Large doses of *curare* paralyse the inhibitory fibres. *Digitalis* excites the vagus centre in the medulla, and thereby reduces the rapidity of the heart's beat.

THE ACCELERATOR NERVES.

After the possibility of increase of blood pressure has been removed by section of the splanchnic nerves, and the tonic inhibition of the vagi has been cut off, it has been found that stimulation of the cervical portion of the spinal cord causes quickening of the heart beat. In the cervical portion of the spinal cord nerve channels must then exist which are capable of stimulating the muscle fibres of the heart, so as to cause it to beat more quickly. These accelerator fibres pass through the communicating branches from the cord to the last cervical or first dorsal sympathetic ganglion, and thence to the heart. Stimulation of the ganglia, or the branches passing thence to the heart quickens its beat. The effect of stimulus applied to these nerves does not begin to show itself until a comparatively long time after it has been applied, and the acceleratory effort continues for a considerable time after the stimulus is removed. Stimulation of the accelerator fibres has little effect on the tonic inhibition of the vagus, which takes place equally well whether the accelerators are stimulated or not, while the action of the accelerators is totally suspended so long as the vagus is being stimulated.

AFFERENT CARDIAC NERVES.

Besides these nerve channels bearing impulses to the heart, others pass from the heart to the medulla, probably having their origin in the inner lining of the heart, which is known to be the part most sensitive to stimulus.

These fibres appear to be of two kinds, one of which affects the cardio-inhibitory centre and diminishes the pulse rate; the other affects the vaso-inhibitory centre and lowers the blood pressure. Increase of the intra-ventricular pressure stimulates both these sets of fibres, and thus we see that over-filling of the heart from increase of blood pressure, &c., causes retardation of its beat, and an equilibrium is thus established between the general blood pressure and the force of the heart-beat.

CHAPTER XVII.

THE BLOOD VESSELS.

THE channels which carry the blood throughout the body form a closed system of elastic tubes, which may be divided into three varieties :—

1. Arteries.
2. Capillaries.
3. Veins.

The arteries and veins serve merely to conduct the blood to and from the capillaries, where the essential function of the blood, *viz.*, its chemical interchange with the tissues, is carried on.

The arteries are those vessels which carry the blood from the heart to the capillaries. The great trunk of the aorta, which springs from the left ventricle, gives off a series of branches, which in turn subdivide more and more freely in proportion to their distance from the heart. Their mode of division is commonly dichotomous, but, from the larger trunk, branches of unequal and irregular size are frequently given off.

Arterial twigs of considerable size here and there form connections with those of a neighbouring trunk (*anastomoses*), but these unions are simple junctions of single branches, never being worthy of the name of a network or plexus, such as those seen in the capillaries or in the veins. The walls of the arteries are made up of three coats :—1. An external tough fibrous layer which gives strength to the vessels,—like the webbing in the wall of rubber water-hose—and acts as a bond of union between it and the neighbouring tissues. This coat (*tunica adventitia*) carries the minute vessels, necessary for the nutrition of the vessel wall, and nerves. 2. The middle coat (*tunica media*) forms the more characteristic part of the arterial structure, being a mixture of pure elastic tissue and unstriated muscle. It is much thicker in the arteries than in the veins, where its special functions are not required. It differs essentially in character in the larger and smaller arteries, the change occurring gradually on passing along the diminishing branches. In the large arteries and the arterioles the middle coat differs much in structure, and in both it forms the most important part for the due performance of their respective functions. In the large vessels it is made up of elastic fibres of various shapes, and sheets of elastic tissue woven into a dense felt-work, interspersed with a few muscle cells. In the small arteries (arterioles) the great mass of the middle coat is made up of muscle cells, the elastic tissue being but sparsely represented. Between the large arteries and the capillaries every grade of transition between these two extremes may be found; the elastic tissue gradually becoming less abundant and the muscle elements more important in proportion as the capillaries are approached. 3. The internal lining (*tunica intima*) of the arteries is composed of a delicate elastic homogeneous membrane lined with a single layer of endo-

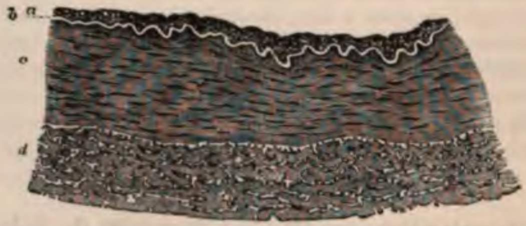


Fig. 124.—Transverse Section of part of the Wall of the Posterior Tibial Artery (man). (Schäfer.)

(*a*) Endothelium lining the vessel, appearing thicker than normal from the contraction of (*b*) the elastic layer of the intima.
(*c*) Middle coat composed of muscle fibres and elastic tissue.
(*d*) Outer coat consisting chiefly of white fibrous tissue.

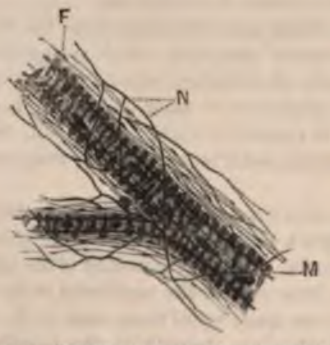


Fig. 125.—Portion of Small Artery from Submucous Tissue of Mouse's Stomach, stained with gold-chloride, showing the nuclei of the muscle cells (M) passing transversely around the vessel to form the middle coat, outside which is the fibrous tissue of the outer coat (F). Around the vessel several fine nerve fibrils form a network (N).

thelial cells. The intima may be said to be continuous throughout all the vessels and the heart cavities.

It is thus seen that the large arteries have extremely elastic and firm walls, capable of sustaining considerable pressure. The smaller the arteries become in calibre the more the general property of elasticity and resiliency is reinforced by that of *vital contractility*, due to the greater relative number of muscle cells contained in the middle coat.

The frequently branching arterioles finally terminate in the capillaries, in which distinct branches can no longer be recognized but these thin canals are united and interwoven into a network of blood channels, the meshes of which are all made up of vessels having about the same calibre. They communicate indefinitely with the capillary meshworks of the neighbouring arterioles, so that any given capillary area appears to be one continuous network of tubules, connected here and there with distinct arterioles, and thus is fed with blood from several different sources. The walls of the capillaries are soft and elastic and permeable not only to the fluid portion of the blood, but also, under certain circumstances, to the solids.

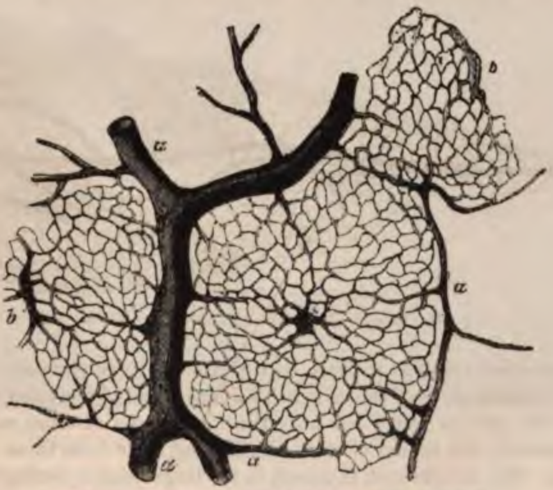


Fig. 126.—Capillary network of a Lobule of the Liver.

It is, in fact, in this part of the circulation that its essential function is carried on, viz., the establishment of a free interchange between the tissues and the blood.

The characters of the capillary network vary in different tissues and different organs; the closeness and wideness of the meshes may be said to be in proportion to the functional activity or inactivity of the organ or tissue in question, a greater amount of blood being required in the parts where energetic duties are performed.

The venous radicles arise from the capillary network, commencing as tributaries which unite in much the same way as the arterioles divide, but they form wider and more numerous channels. They rapidly congregate into comparatively large vessels, which frequently intercommunicate so as to form coarse and irregular plexuses. The general arrangement of the structures in the walls of the veins is like that of the arteries; they also have three coats, the external, middle, and internal; the tissues of each differing but little from those of the arteries. The middle coat, however, in the large veins is distinguished from that of the large arteries by being much thinner, owing to the paucity of yellow elastic tissue. It is also characterised by its relative richness in muscle fibre, while the structure of the middle coat of the small veins can only be distinguished from that of the arterioles by the comparative sparseness of the muscle cells running around the tubes.

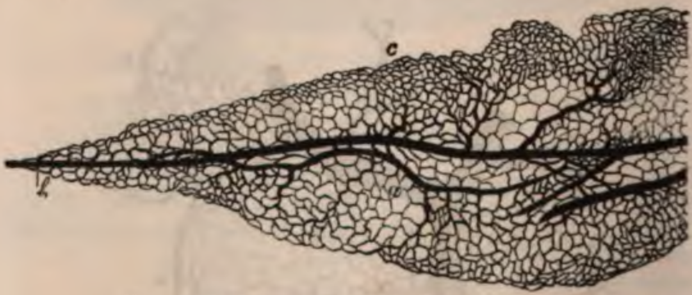


Fig. 127.—Capillary network of Fat Tissue. (Klein.)

The veins are capable of considerable distension, but, though possessed of a certain degree of elasticity, they are much inferior to the arteries in resiliency.

In a large proportion of veins, valve-like folds of their lining coat exist which prevent the backward flow of blood to the capillaries, and insure its passage towards the heart. These valves resemble in their general plan the pocket valves that protect the great arterial orifices of the heart. They vary much in arrangement, there being commonly but two or sometimes one flap or pocket entering into the formation of the valve. They are most closely set in the long veins of the extremities, in which the blood current has to move against the force of gravity.

The general aggregate diameter of the different parts of the vascular system varies greatly. The combined calibre of the branches of an artery exceeds that of the parent trunk, so that the aggregate sectional area of the arterial tree increases as one proceeds from the aorta towards the capillaries. After the muscular arterioles are passed the general diameter of the vascular system suddenly increases enormously, and in the capillaries it reaches its maximum, which is said to be about eight hundred times as great as the diameter of the aorta.

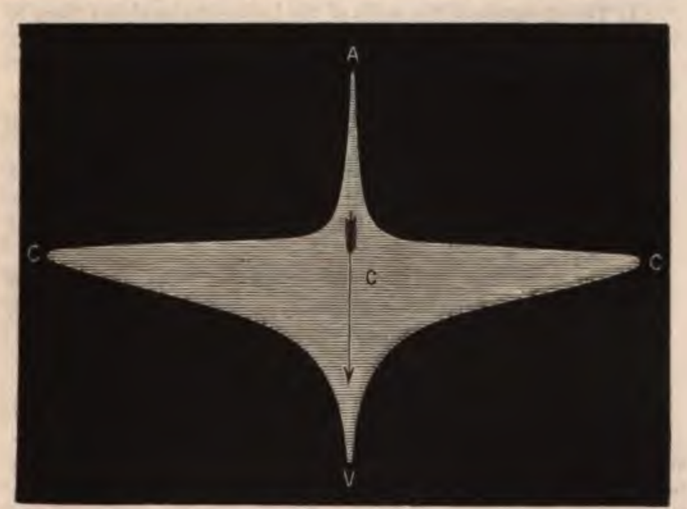


Fig. 128.—Diagram intended to give an idea of the aggregate sectional area of the different parts of the vascular system.

A. Aorta. C. Capillaries. V. Veins.

The transverse measurement of the shaded part may be taken as the width of the various kinds of vessels supposing them fused together.

The aggregate sectional area of the veins also diminishes as the tributaries unite to form main trunks, and reaches its minimum at the entrance of the vena cava into the right auricle.

The capacity of the veins is, however, everywhere much greater than that of the corresponding arteries, the least difference being near the heart, where, however, the calibre of the veins is more than twice that of the aorta.

After this brief anatomical sketch the most important properties of each different part of the vascular system may be summarised thus :—

1. The structure of the walls of the large arteries shows them to be capable of sustaining considerable pressure, and of exerting powerful *elastic recoil.*
2. In the small arteries, as well as this elasticity, great variability in their calibre, dependent on the contraction of their muscular coat, occurs.
3. In the capillaries we find extreme thinness, elasticity, and permeability of their wall, which presents an enormous surface, so as to allow free interchange between the blood and the surrounding textures.
4. The veins have yielding and distensible coats, great general capacity to accommodate a large quantity of blood, and valves to prevent its backward flow upon the capillaries.

Physical Forces of the Circulation.

When liquid flows through a tube it does so as the result of a difference of pressure in the different parts of the tube ; the liquid moving from the part where the pressure is higher towards that where it is lower.

The energy of the flow corresponds with the amount of difference in the pressure, and varies exactly with the pressure-difference, being continuous so long as the pressure is unequal in different parts, and being interrupted when the pressure is equalised throughout the tube. If liquid be forcibly pumped into one extremity of a long tube, such as a garden hose, a pressure difference is of course established, the pressure becoming greater at the end into which the liquid is pumped, consequently a current takes place towards the open end. So long as the free or distal end of the tube is quite open and on the same level as the rest, no very great increase of pressure can be brought to bear on the walls of the tube, no matter how forcibly the pumping may go on, as the liquid easily escapes, and therefore flows out all the more quickly as the pumping becomes more energetic. If, however, the outflow be impeded by raising the distal end of the tube to any considerable height, or by partially closing the orifice with a nozzle or rose, then the pressure within the tube can be greatly increased by energetic pumping, and the tube being elastic will swell when distended by the pressure.

It can be further observed in this common operation that the smaller the orifice of the nozzle be, the greater the pressure in the tube with a given rate of working the pump; and, the orifice remaining the same, the pressure will increase in proportion as the pump is more energetically worked. Or in other words, the pressure within the tube will depend on (*a*) the force used at the pump, and (*b*) the degree of impediment offered to the outflow.

If the tube be resilient, and if the nozzle have a small orifice so that a high pressure can be established within the tube, it will be found that the liquid will flow from the nozzle in a continuous stream, and will not follow the jerks communicated by the pump. That is to say, the interrupted energy of the pump is stored up by the elastic tube and converted into a continuous *pressure* exerted on the fluid. But if the tube be quite rigid, or the orifice too wide to allow the pressure within the tube to be raised sufficiently high, then the fluid will flow out of the end of the tube in jets which correspond with the strokes of the pump: that is to say, the outflow will follow closely the pressure difference caused by the pump at the point of inflow.

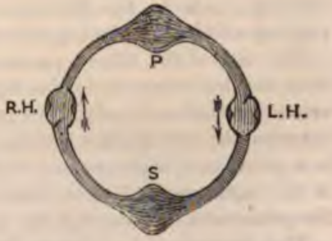


Fig. 129.—Diagram of Circulation, showing right (R.H.) and left (L.H.) hearts, and the pulmonary (P) and systemic (S) sets of capillaries.

Now these simple facts (which can be verified experimentally with an ordinary enema bag, a yard of elastic tubing, and a short glass tube drawn to a point) form the key to the most important dynamic principles of the circulation.

The cause of the blood's motion is simply a difference in the pressure within the various parts of the vascular system, for the heart acts as the pump filling the tube represented by the large elastic arteries, which can be more or less distended, according as (1) the outflow is impeded or facilitated by the contraction or relaxation of the muscular arterioles which form the outlet, or as (2) the inflow is increased or diminished by the greater or less activity of the heart's action.

From the foregoing facts, and what has been said of the direction of the blood current, namely, that it flows from the arteries through the capillaries into the veins, it would then appear that the pressure in the arteries exceeds that in the capillaries, and the pressure in the capillaries must in turn be greater than that in the veins, the blood flowing in the direction in which the pressure becomes less.

The difference in the manner in which the blood flows from a cut artery and a cut vein shows that a great difference exists in the pressure within the two sets of vessels.

When a small artery is cut across and the orifice directed upwards the blood is thrown two or three feet in jerks. When a vein is cut, the blood only trickles gently from its orifice, the force depending much upon the position of the part ; and it is well known that bleeding from a vein in the leg can easily be stopped by placing the limb in a position more elevated than the rest of the body, so as to remove the force of gravity from acting on the blood.

By means of a special form of gauge (the mercurial manometer) —which will presently be described—the exact difference in the pressure exerted by the blood against the vessel walls in the different parts of the circulation can be accurately estimated, and it has been found by direct experiment that the blood-pressure varies just as one would be led to expect from a consideration of its physical relationships, namely, the direction and rate of the current and the varying width of the bed in which it flows.

The rate of the fall in pressure observed in the vessels passing from the left ventricle to the right auricle is not even, but in the arterioles it falls suddenly, and a great difference therefore always exists between the arterial and venous pressure (v. p. 240). Since there is a permanent high pressure in the arteries as compared with that in the capillaries and veins, there can be no difficulty in explaining the permanent flow through the capillaries from arteries to veins.

The fundamental problem that must be clearly understood in studying the dynamics of the circulation is, how the high pressure in the arteries is kept up, or, in other words, how the arteries can exert so much pressure on the blood when the capillary out-flow is so wide and free.

From the description already given of the action of the heart, it appears that each beat of the ventricle pumps some six ounces of blood into the aorta, which blood, though coming to the left ventricle from the pulmonary circulation, may, on account of the exact co-operation of the two sides of the heart, be said to be pumped out of the systemic veins, and thus, as far as the physical forces are concerned, the pulmonary circulation may be left out of the question. This occurs some seventy times a minute, so that an enormous quantity of blood is removed from the veins and forced into the arteries. The ventricles in filling the arteries have to work against considerable pressure, and may be said to pump the blood from the low-pressure veins up into the high-pressure arteries, and this work is the cause of the pressure difference between the two sets of vessels. During the contraction of the heart the ventricular pressure must exceed that of the aorta, while during the diastole it falls to that of the auricle or even of the great veins. The heart then is the first and most important agent by which the arteries are kept stretched and over-filled, and the veins are emptied.

A second important factor in enabling the high blood-pressure to be kept up, is the resiliency of the middle coat of the arteries. It is only on account of the great elasticity of the arterial walls, that these vessels are capable of being so over-filled, and only on account of the perfect resiliency of the elastic coat, that they are able to exert such powerful pressure on the blood for such an unlimited time. If the arteries were rigid tubes, overfilling them with a fluid itself inelastic would be out of the question ; the outflow from the distal extremity would take place exactly when the additional charge of blood was injected by the heart.

With each contraction the ventricle overcomes arterial pressure, and further stretches the elastic artery. But the act of injecting the blood into the aorta only occupies about one quarter of each heart beat. The semilunar valves bear the pressure of the blood in the aorta for the rest of the time. The whole force of the ventricle is therefore used up in causing arterial distension. During the greater part of the time (about three-quarters of the heart's cycle), the arteries are in the condition of over-filled elastic tubes, with their cardiac end firmly closed by the aortic valves, and their distal ends open.

It follows that the blood flowing constantly out of the distended arteries through the capillaries into the veins tends to equalise the pressure in the veins and arteries. But why is not this constant outflow sufficient to allow the pressure in the arteries to fall to the level of that in the veins ? Or in other words, what is the impediment offered to the escape of the blood from the arteries that thus keeps them distended ? If the arteries and veins were a set of continuous wide tubes of similar construction and capacity throughout, it would be impossible for the heart to empty the veins, to overfill the arteries, and to establish the great pressure difference that normally exists. Therefore some resistance equal to the pressure must be offered to the flow of the blood from the arteries into the veins.

This resistance is made up of several items, of which one alone is sufficient to keep up the arterial pressure, namely, the active contraction of the arterioles. No doubt the enormous increase of surface over which the blood has to move in the capillaries, and the pressure exercised upon them by the surrounding elastic tissues, impede the emptying of the arteries. But that the contractility of the arterioles is the most important item, may be seen from the following consideration. The resistance offered by the capillaries themselves, whether by the greater friction or by the elastic pressure, is insignificant when compared with the arterial blood pressure, and is far from sufficient to restrain the blood from rushing into the veins. This is seen when the arterioles are paralysed by the destruction of the nervous mechanism controlling them ; the blood then flows readily through the capillary network, the veins become engorged, the arterial blood pressure falls, and the circulation comes to a standstill, in spite of the heart's more rapid beats. We know also that after the arterioles are passed the pressure falls suddenly, and in the capillary network the pressure is always very low.

The four great factors then, in keeping up the arterial blood-pressure, are : 1, the heart-beat ; 2, perfect aortic valves ; 3, the elastic resiliency of the large arteries ; 4, the resistance offered by the contraction of the muscular arterioles.

If any of these fail, the mechanism of the circulation is at once impaired. For example, the heart's beat may be stopped by the stimulation of the inhibitory nerve fibres of the vagus, in which case the blood pressure rapidly falls, as shown by the curve taken by the graphic method. Or weakness of the heart-beat may arise from disease (fatty degeneration) of the muscle, when signs of low arterial tension can be recognised in the human subject.

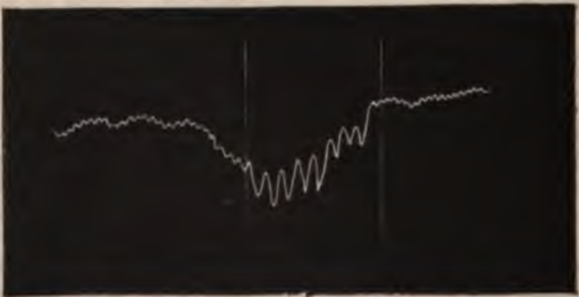


Fig. 130.—Tracing, showing the effect of Stimulation of Vagus Nerve. Stimulus applied between vertical lines. (Recording surface moved from left to right.)

Any insufficiency of the aortic valves, whose duty it is to close the proximal end of the arteries, that permits the blood to flow backward into the ventricle, allows the pressure in the arteries to fall between each ventricular systole, so that the characteristic "pulse of unfilled arteries" is recognised by the physician.

The resiliency of the arterial coats may also be destroyed to a certain extent by degeneration of the tissue, in which case the large arteries become greatly distended, and unable to exert their normal steady pressure on the blood.

Injuries of the nerve centres are often associated with paralysis of the muscular arterioles, and fall of blood pressure; but the effect upon the blood pressure of dilatation of the small arteries can be best seen by experimenting on the nerves that control their contraction in the lower animals. If paralysis or inhibition of the vasomotor mechanisms be experimentally produced, the result on the arterial pressure is the same, namely, a sudden fall, which may reach zero: all opposition to the outflow of blood from the arteries being stopped, they cease to be tense, even though the ventricle continue to beat and pump the blood into them.

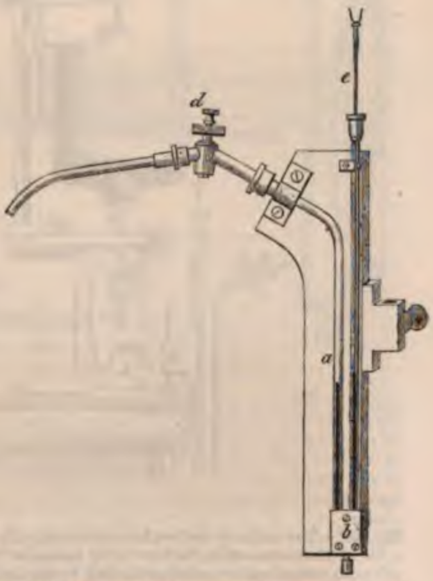


Fig. 131.—Mercurial Manometer for measuring and recording the blood pressure.

- *a*. Proximate limb of manometer.
- *b*. Union of two limbs of manometer.
- *e*. The rod floating on mercury and carrying the writing point.
- *d*. Stop-cock through which the sodium bicarbonate can be introduced between the blood and mercury of manometer.

MEASUREMENT OF THE BLOOD PRESSURE.

The first attempt at direct measurement of blood pressure was made by the Rev. Stephen Hales about the middle of last century, who, wishing to compare the motion of fluids in animals with that of plants, connected a tube in an artery of a living animal, and found that the blood was ejected with considerable force, and that when the artery of a horse was brought into union with a long upright tube, the blood reached a height of about three yards.

The blood itself is not now used as a measure, because so much blood leaving the vessels tends to empty them and to reduce the pressure in the arteries; besides the coagulation of the blood soon stops the experiment. We now employ the mercurial manometer, which consists of a column of mercury in a U-shaped tube. To prevent coagulation, the tube between the mercury and blood is filled with a solution of sodium carbonate, the pressure being regulated to equalize as nearly as possible that of the blood. A rod is made to float upon the mercury, in the open side of the tube, and to the upper extremity of this a writing apparatus can be attached, so that by the movements of the mercury, a graphic record of the blood pressure and its variation can be traced on a regularly moving surface.

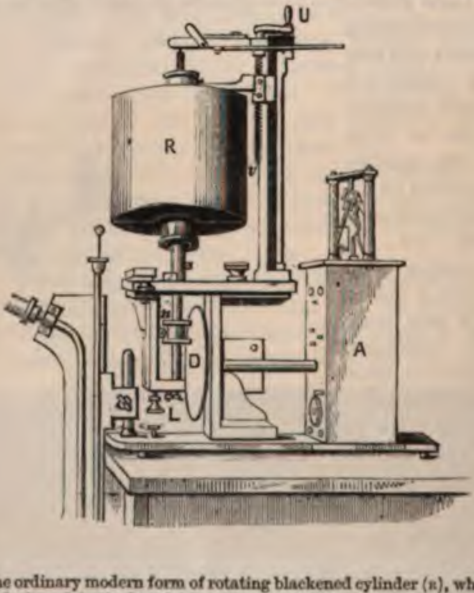


Fig. 132.—The ordinary modern form of rotating blackened cylinder (R), which is moved by the clockwork in the box (A) by means of the disc (D) pressing upon the wheel (W), which can be raised or lowered by the screw (L), so as to rub on a part of the disc more or less near the centre, and thus rotate at different rates. The cylinder can be raised by the screw (S), which is turned by the handle (U). (Hermann.)

This instrument, known as Ludwig's Kymograph, is that used in all ordinary measurements and experiments on blood pressure. In order to overcome the inertia of the mercurial column, another instrument has been devised which will be mentioned in speaking of the character of the curve (p. 242). When an experiment of long duration has to be made, a recorder with a long rolled strip of paper can be employed (Fig. 133).

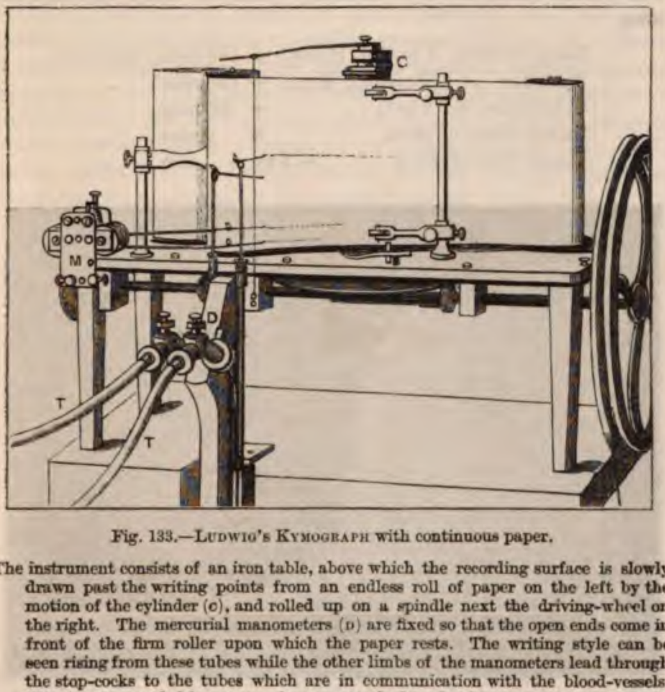


Fig. 133.—Ludwig's Kymograph with continuous paper.

The instrument consists of an iron table, above which the recording surface is slowly drawn past the writing points from an endless roll of paper on the left by the motion of the cylinder (c), and rolled up on a spindle next the driving-wheel on the right. The mercurial manometers (d) are fixed so that the open ends come in front of the firm roller upon which the paper rests. The writing style can be seen rising from these tubes while the other limbs of the manometers lead through the stop-cocks to the tubes which are in communication with the blood-vessels. The time is recorded by means of a pen attached to the electro-magnet (m), which, by a "breaking" clock, is demagnetised every second. The moment at which a stimulus is applied is marked by a key to which another pen is attached near the time-marker.

The modern accurate methods of research have taught us the differences in pressure that exist in the various parts of the vascular system. However, direct measurement can only be accomplished in vessels of such a size as to admit a cannula, hence the pressure in the capillaries in the very minute arteries and veins, can only indirectly be estimated. The pressure in all parts of the vascular system is subject to frequent variations to be presently mentioned, but this table may be useful in giving a general idea of the average permanent differences that exist in the different vessels of large animals and man.

Large arteries	(Carotid, Horse)	+ 160 mm.,	mercury
Medium „	(Brachial, Man)	+ 120 mm.,	„
Capillaries of Finger,		+ 38 mm.,	„
Small Veins of Arm		+ 9 mm.,	„
Large Vein of Neck		– 1 to – 3 mm.,	„

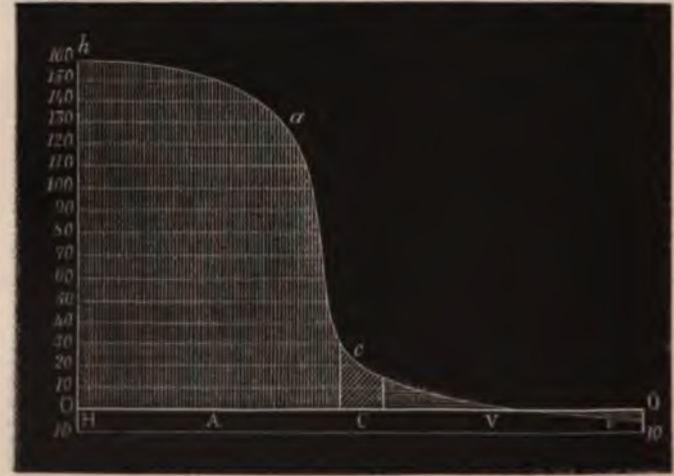


Fig. 134.—Diagram showing the relative height of the blood-pressure in the different regions of the vessels.

H. Heart.
A. Arteries.
a. Arterioles.
c. Capillaries.
v. Small veins.
V. Large veins.

H. V. being the zero line, the pressure is indicated by the elevation of the curve. The numbers on the left give the pressure (approximately) in mm. of mercury.

If the different parts of the circulation be represented on the base line H. A. C. V., these letters corresponding to heart, arteries, capillaries, and veins respectively, and if the height of the blood pressure be represented on the vertical line in mm. Hg. the curve *h, a, c, v*, would give about the relative pressure in the various parts of the circulation. This shows that in the receiving chamber of the heart the pressure is below zero, while the ventricular pump drives it to the height of the arterial pressure 160 mm. Hg. In the arteries the pressure though gradually falling is everywhere high, while just before the blood reaches the capillaries, a sudden fall occurs. The variation after this is merely a gentle descent until the large venous trunks are reached, where the pressure is below zero. From a purely physical point of view then, the ventricle may be regarded as pumping the blood up to an elevated high-pressure reservoir of small capacity (the arteries), from which it rapidly falls by numerous outlets into an expansive low-lying irrigation basin (the wide capillaries), whilst it slowly trickles back to the well (the auricle) under the pump, which lies below the surface pressure.

From this diagram the following points can be gathered :—

1. The great difference between the pressure on the arterial and venous sides of the circulation.
2. The comparatively slight difference in pressure in the different parts of the arterial or of the venous systems respectively.
3. The suddenness of the fall in the pressure between the small arteries and the capillaries, where the great resistance to the outflow is met with.
4. In the large veins the pressure of the blood is habitually below that of the atmosphere, only becoming positive during forced expirations.

VARIATIONS IN THE BLOOD-PRESSURE.

If the blood pressure be recorded with Ludwig's Kymograph, a tracing will be obtained, which shows that the pressure undergoes periodic elevations and depressions of two different kinds. The smaller oscillations are found to correspond with the heart-beat, the larger waves have the same rhythm as the respiratory movements, and the average elevation of the mercurial column is spoken of as the *mean pressure*. In the large arteries of the warm-blooded animals, this mean pressure varies with the size of the animal from 90 mm., mercury, to more than 200 mm. In cold-blooded animals it is comparatively low, from 22 mm. (frog, Volkmann), to 84 mm. (large fish).

The general mean pressure in the arteries is increased by : (1), increased action of the heart ; (2), increased contraction of the muscular coat of the arteries; (3), sudden increase in the quantity of blood. When the change is gradual, the vessels adapt themselves to the increase. The opposite of these conditions may be said to have an opposite effect.

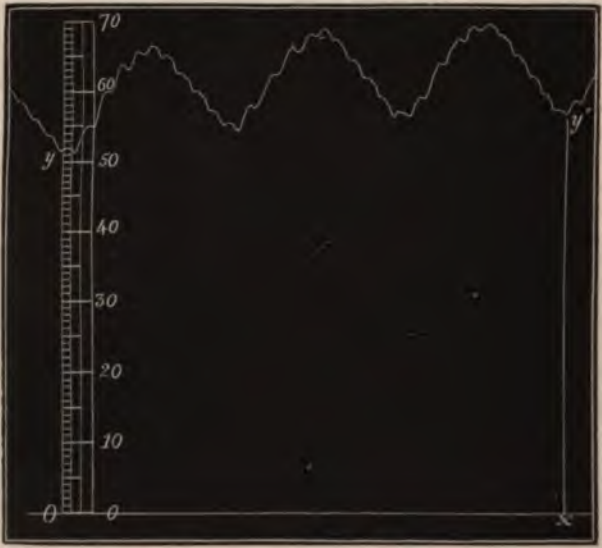


Fig. 135.—Blood-pressure Curve, drawn by mercurial manometer. O—x = zero line. y—y' = curve with large respiratory waves and small waves of heart impulse. A scale is introduced to show height of pressure in c c of Hg.

The character of the change in pressure which accompanies the heart's systole, is not exactly shown in the tracing obtained by the mercurial manometer, owing to the sluggishness of the movement of the mercurial column which, as it were, rubs off the apices of the curves. But with the spring Kymograph of Fick, the details of these oscillations are marked. They are of course synchronous with the arterial pulse, and follow the variations of tension, as will be described when treating of that subject. (See Figs. 136 and 137.)

The cause of the undulations in the blood-pressure curve corresponding to the respiratory movements is not quite so simple as it might appear to be at first sight, and it has often been misunderstood. Though many causes have been given, no single one appears to explain adequately all the changes that may occur in this phenomenon under varying circumstances. At first sight the respiratory movements and consequent pressure changes within the thorax would seem to give a

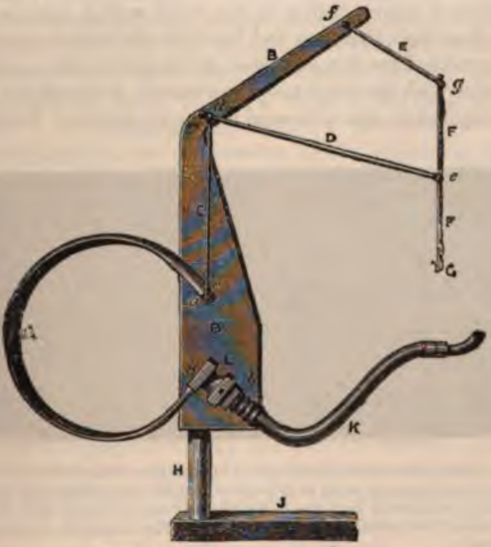


Fig. 136—Fick's Spring Manometer.

A hollow C-shaped spring (A), made of extremely thin metal, is fixed at (*b b*) where its cavity communicates with the tube (K). The top of the C is connected at (*a*) with the writing lever. Any increase of pressure in the tube (K) causes the spring to expand and move the writing point (*a*) up and down.

simple mechanical explanation. But if the change occurring in the intra-thoracic pressure be examined carefully, it will be found not to correspond exactly with the so-called respiratory wave of the pressure curve in the arterial system. Owing to the lungs being very elastic and constantly tending to shrink away from the costal pleura, as may be seen when the thoracic cavity is opened and the lungs collapse, the pressure in the pleural cavity is less than that of the atmosphere which distends the lungs, *i.e.*, the pleural pressure is *negative*. All the viscera in the thoracic cavity are habitually under the influence of the negative pressure. Thus the elastic lungs exert a kind

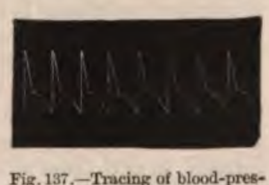


Fig. 137.—Tracing of blood-pressure taken with Fick's manometer.

of traction on the pericardium, and tend to cause a negative pressure within the heart and great systemic vessels, both arteries and veins. The influence is of course greater in the thin walled veins in which the pressure is minimal, than in the thick walled arteries where the pressure is so high, that they feel but little the intrathoracic decrease.

The amount of traction exercised on the pericardial contents by the lungs varies with the respiratory movements, being slightly increased during inspiration, and decreased during expiration. The differences which are thus produced however during ordinary respiration are very slight (probably 1 mm., mercury), when compared with the mean negative pressure, which, while the thorax is in an intermediate state of extension, is probably about 10 mm., mercury. So slight a variation as 1 mm., mercury, could not, by direct action on the aortic arch, cause the change of several millimetres which we see in the respiratory undulation in the arterial pressure. We must, therefore, seek the explanation in the changes it causes in the great veins.

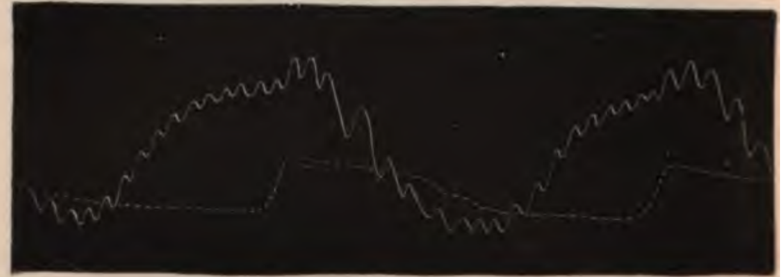


Fig. 138.—Blood-pressure and Respiratory Tracings recorded synchronously—recording surface moving from right to left—showing that the variations in pressure in the arteries (continuous line) and in the thoracic cavity (dotted line) do not exactly correspond, the latter continuing to fall after the blood pressure has commenced to issue.

It has been suggested that by facilitating the flow from the great veins into the thorax, by a kind of sucking action, the amount of blood entering the right auricle during inspiration may be increased, and thus the left ventricles may be better filled and made to beat more actively, so as to cause an elevation in the arterial pressure.

But this view appears to leave the pulmonary circulation out of the question in a way hardly justifiable, since it must be traversed by the blood before the increased inspiratory inflow to the right auricle can affect the left ventricle or the systemic arteries.

The sequence of events may be read as follows. During inspiration the negative pressure on the right heart is increased; the atmospheric pressure acting on the tributaries of the superior vena cava is unchanged, while the pressure in the abdominal cavity is increased, and the inferior vena cava compressed by the muscular action. The blood then flows more readily during inspiration into the right heart, and consequently the lungs receive a larger supply of blood during this period. In expiration the negative intrathoracic pressure becomes less negative, the compression of the abdominal viscera is relieved, and the flow into the auricle loses somewhat in force.

It must be carefully borne in mind that the left side of the heart works under different conditions, for the same variations of pressure affect both the pulmonary veins and the left auricle equally, since they are both included in the thoracic cavity, and are both subjected to a slightly varying negative pressure. The aid given to the flow into the right heart by the low intrathoracic pressure is quite absent on the left side; so that the thoracic movements do not exert any influence on the flow of blood from the pulmonary vein to the systemic arteries. But while inspiration is taking place the lungs receive a larger supply of blood; and from the relative amounts of blood in the different organs it is probable that this slight excess, having passed the lungs, arrives at the left ventricle at the period of expiration. Thus, during expiration the left ventricle receives from the lungs and ejects to the systemic arteries an amount of blood slightly in excess of that which it receives and ejects during inspiration. This may have a direct effect on the pressure in the great arterial trunks. But it is more than probable that excess of blood in the heart cavities acts as a nervous stimulus, and excites the inhibitory centre of the heart and the depressor centres which control the arterioles.

The adoption of this view appears necessary from the following facts:—

(1.) The rise in pressure is not exactly synchronous with expiration or inspiration:

(2.) The heart beats more slowly during expiration than inspiration:

(3.) This difference at once disappears if the vagi be cut, and the respiratory wave becomes greatly modified:

(4.) The respiratory wave is observed when artificial respiration is employed, in which the forcing of air into the lungs is the *cause*, and not the *result*, of the thoracic movements, so that the pressure effects are reversed.

We may conclude, then, that a sympathy in action can be distinctly recognised in the working of the respiratory and cardiac nerve centres.

Since the undulations known as Traube's curves occur in curarised animals when no respiratory movements are performed, it has been proposed to explain the respiratory undulations in the same way, namely, by referring them to a stimulation of the vasomotor centre by impure blood, which by rhythmical impulses increasing the contraction of the arterioles causes a rhythmical variation in the blood pressure. This explanation seems to be rendered unsatisfactory by the fact that the respiratory undulations go on even when the arterioles are cut off from their chief nerve centres by sections of the spinal cord. So that if these undulations are to be referred to nerve mechanism we are ignorant of the course the nerve impulses take, for any rhythmical sympathy existing between the respiratory and vasomotor nerve centres in the medulla cannot have any influence when the cord is cut.

The blood-pressure in the capillaries cannot be directly measured; it is difficult to estimate, and very variable. The slightest change of pressure in the corresponding veins or arteries causes the pressure in the capillaries to rise or fall. Thus, variations in pressure are constantly occurring in the capillaries, which cause an alteration in the rate of flow, or even a retrograde stream in some parts of the network.

The regulation of the blood-supply, and, therefore, of the pressure in the capillaries, is under the control of the small arterioles which supply them; a slight relaxation of the muscle of the arterioles causes great increase in the amount of blood flowing through the capillaries, as can readily be seen with the microscope.

The blood-pressure in the veins must be less than that in the capillaries, and, as has been said, must diminish as the heart is approached, where in the great veins (superior cava) the pressure is said to be rather below that of the atmosphere (-3 to -5 mm., mercury). During inspiration the minus pressure may become much less, whilst, on the other hand, it is only by very forced expiration that it ever becomes equal to or at all above that of the atmosphere.

This is a most important fact, as the suction considerably helps the flow of blood from the veins, and also the current of fluid from the thoracic duct that bears the chyle from the intestines and the fluid collected from the tissue drainage back to the blood.

The pressure of the blood in the veins may then be said to be generally *nil*, since the veins are nowhere over-filled with blood. The pressures, on the other hand, that can be registered and measured depend upon forces communicated from without, namely: (1) gravity; (2) the elastic pressure of the surrounding tissue; and (3) the pressure exerted by the muscle during contraction. This pressure is increased by any circumstance which impedes the flow of blood through the right side of the heart, through any large vein, or through the pulmonary circulation; but when no abnormal obstacle exists to the venous blood-current the pressure in those vessels can never attain any great height, for, as we have seen, the large trunks are constantly being emptied by the heart's action.

Most circumstances which tend to lower arterial pressure also tend to raise the pressure in the veins, so that, when the heart's action is weak, or its mechanism faulty, the venous pressure rises.

In the veins of the extremities the pressure greatly depends on the position of the limb, as it varies almost directly with the effect of gravity.

In the pulmonary circulation the direct measurement of the intravascular pressure is rendered extremely difficult, and possibly erroneous, by the fact that to ascertain it the thorax has to be opened. It has been found in the pulmonary artery to be in a dog 29·6 mm., in a cat 17·6 mm., and in a rabbit 12 mm., mercury.

THE ARTERIAL PULSE.

Each systole of the ventricle sends a quantity of blood into the aorta, and thus communicates a stroke to the blood in that vessel. The incompressible fluid causes the tense arterial wall to distend still further, and the shock to the column of blood is not transmitted onward directly by the fluid, but causes the elastic walls of the arteries to yield locally, and thus it is converted into a wave which passes rapidly along those vessels. This motion in the walls of the vessel can be felt wherever the artery can be reached by the finger, but best—as in the case in the radial and temporal arteries, where the vessel is superficial and lies on some unyielding structure such as bone.

This motion of the vessel wall is called the arterial pulse. It consists of a simultaneous widening and lengthening of the artery. The arteries near the heart are much more affected by the pulse wave than those more remote, the wave becoming fainter and fainter as it travels along the branching arteries. In the smallest arteries it is hardly recognisable, and under ordinary circumstances is quite absent in the capillaries and veins.

The diminution in the pulse-wave in the smaller arteries chiefly depends upon the fact that the force of the wave is used up in distending the successive part of the arteries. In the small arteries the extent of surface to which the pulse-wave is communicated is enormous, and thereby the wave is much decreased. Moreover, it is probable that reflected waves pass from the peripheral end of the arterial tree, and meeting the pulse-wave in the small arteries help to obliterate it.

The pulse-wave can easily be shown to take some time to pass along the vessels. Near the orifice of the aorta the arterial distension occurs practically at the same time as the ventricular systole, but even with comparatively rough methods the radial pulse can be observed to be a little later than the heart-beat. The difference of time between the pulse in the facial and the dorsal artery of the foot has been estimated to be one-sixth of a second, and the difference in the distance of these vessels from the heart is about 1,500 mm., so that the rate at which the pulse-wave travels is nearly 10 metres per second. The velocity of the wave is said to be regulated by the degree of elasticity in the walls of the vessels, and it would appear to be quicker in the lower than in the upper extremity.

The time that the wave takes to pass any given point must be equal to the time taken to produce it, that is to say, the time the ventricle occupies in sending a new charge of blood into the aorta, which is about one-third of a second. Knowing the rate at which the wave travels (10 m. per sec.) and the time it takes to pass any given point ($\frac{1}{3}$ sec.) its length may be calculated to be about three metres, or about twice as long as the longest artery. Thus the pulse wave reaches the most distant artery in one-sixth of a second, or about the middle of the ventricular systole, and when the wave has quite passed from the arch of the aorta, the summit of it has only just reached the arterioles.

Numerous instruments have been invented for the demonstration and graphic representation of the pulse in the human being. Of these the one most commonly used is Marey's Sphygmograph (Fig. 139), by means of which a graphic record of the pulse is made, in the form of a tracing of a series of elevations and depressions (Fig. 140). The elevations correspond to the onset of a wave, and the depressions to its departure, or to the temporary rise and fall of the arterial pressure. In the falling part of the curve an irregularity caused by a slight second wave is nearly always seen. This is called the *dicrotic* wave. Sometimes there are more than one of these secondary waves, the most constant of which is a small wave preceding the dicrotic, called *predicrotic;* but the dicrotic is always more marked than any other. Several waves of oscillation can be seen as a gradually decreasing series in tracings taken from elastic tubes, but we cannot say positively that they occur in the arteries. When several secondary waves exist in the pulse curve the smaller ones probably depend on oscillation caused by the lever of the instrument.

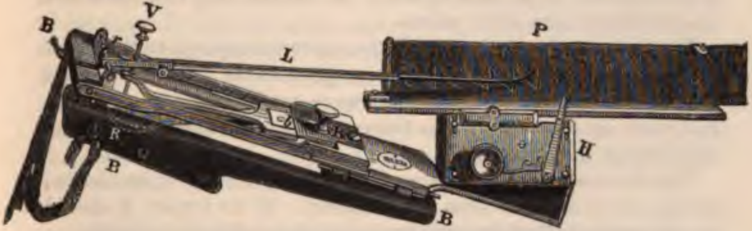


Fig. 139.—Marey's Sphygmograph.

The frame (B, B, B) is fastened to the wrist by the straps at B, B, and the rest of the instrument lies on the forearm. The end of the screw (V) rests on the spring (R), the button of which lies on the radial artery. Any motion of the button at R is communicated to V, which moves the lever (L) up and down. When in position, the blackened slip of glass (P) is made to move evenly by the clockwork (H) so that the writing point draws a record of the movements of the lever.

The dicrotic wave does not depend on the instrument, because the skilled finger laid on the radial artery at the wrist can easily detect it, and it can be directly seen in the vessel when the pulsation in the arteries is visible, or when a jet of blood escapes from an artery.

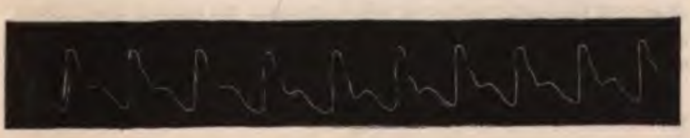


Fig. 140.—Tracing drawn by Marey's Sphygmograph. The surface moved from right to left. The vertical upstrokes show the period when the shock is given by the systole of the ventricle. The upper wave on the downstroke shows when the blood has ceased to enter the aorta. Then comes the dicrotic depression which is a negative wave produced by the momentary backflow in aorta, and the dicrotic elevation caused by the closure of the valves.

When a new charge of blood is shot into the aorta the elastic wall of the vessel is suddenly stretched. At the same time a shock is given to the column of blood, and the fluid next the valves is moved forwards with great velocity. Owing to its inertia the fluid tends to pass onwards from the valves, and thus allows a momentary fall in pressure which is at once followed by the reflux of the blood and the forcible closure of the valves.

The first crest or apex of the pulse curve corresponds to the shock given by the systole, and is greatly exaggerated by the inertia of the lever. The crest of the predicrotic wave marks the moment when the blood ceases to flow from the ventricle, and therefore it is the real head of the pulse wave.

The dicrotic wave has been explained as (1) a wave of oscillation, or (2) a wave reflected from the periphery. If the former, it should be less marked than the predicrotic, which by this theory is said to be the first wave of oscillation, for each succeeding oscillation is less than its forerunner. But, as already mentioned, the dicrotic is invariably the larger.

There are many reasons why it cannot be a wave of reflection from the periphery of the arterial tree; viz., 1. Its curve is not nearer the primary wave when the peripheral vessels are approached. 2. The arterioles which form the peripheral resistance are at too irregular distances to give one definite wave of reflection. 3. It is seen in the spurting of an artery cut off from the periphery. 4. It increases with the greater elasticity and low tension, while the reflected waves diminish.

The dicrotic notch depends upon a negative wave caused by the sudden stop of inflow and the momentary reflux of blood before the valves are closed; and the dicrotic crest is no doubt produced by the closure of the aortic valves, at which moment the sudden check given to the reflux of the blood column causes a positive centrifugal wave to follow the primary wave of the pulse.

The view that the reflux of blood and the closure of the valves produce the dicrotic wave is supported by the fact that the conditions which increase the dicrotism—viz. (1) sharp strong systole, (2) low tension, and (3) perfect resiliency—promote the recoil and closure; and, on the other hand, the conditions which diminish the dicrotic wave in the most marked degree, are (1) inefficiency of the aortic valves, and (2) a rigid calcareous condition of the arteries.

It can be shown by means of an elastic tube, fitted with a suitable pump and sphygmographs, that when its outlet is closed a *positive* wave is reflected from the distal end back to the pump, and when it is open a *negative* centripetal wave is reflected. This fact assists us in explaining the variations in the character of the pulse curve of the radial artery where the equidistance of the derived arterioles enables the reflected waves to have considerable effect. When the arterioles are constricted (a condition corresponding to the closed tube) a positive wave centripetal is reflected and is *added* to the pulse-wave so as to diminish the dicrotic notch, and give the curve known as characteristic of "high tension" pulse, as in Bright's disease. (Fig. 141, II.) On the other hand, when the arterioles are widely dilated (corresponding to the open condition of the tube) a negative wave is reflected, and is *subtracted* from the force of the pulse-wave so as to exaggerate the dicrotic notch, and give the tracing characteristic of the "low tension" pulse seen in fever, &c. (Fig. 141, III.)

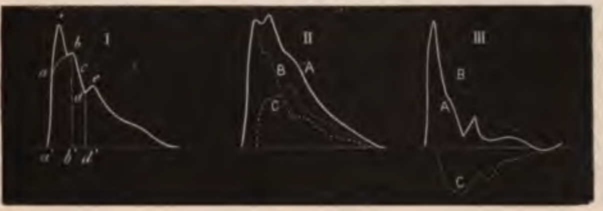


Fig. 141.

I. Scheme of Normal Pulse Curve: *a*, Entrance of ventricular stream into the aorta, the lever is jerked too high to reach *; *ab* shows real summit of waves; *b*, point at which stream from ventricle ceases; *c*, negative wave caused by (1) sudden cessation of inflow and slight reflux of blood; *d*, point of closure of aortic valves; *e*, positive wave from valves (dicrotic wave). The time may be measured on abscissa at *a' b' d'*.

II. Scheme of High Tension Pulse Curve. A. Curve of radial pulse, which is the resultant of *positive* reflected wave C. added to the primary curve B.

III. Scheme of Low Tension Pulse Curve: A. Radial pulse curve, which is the resultant of the *negative* reflected wave C. subtracted from the primary wave B. (After Grashey.)

The mean rate of the pulse varies in different individuals, seventy-two per minute being a fair average for a middle-aged adult. It varies also with many circumstances, which must be borne in mind in taking the pulse as a clinical guide.

1. *Age.* At birth it is about 140 per minnte, and is, generally speaking, quicker in young than in old people, commonly falling to 60 in aged persons.

2. *Sex.* It is more rapid in females than in males.

3. *Position.* It is quicker standing than lying, particularly if a patient who has been lying down, stand or sit up, the pulse becomes more rapid.

4. *The time of day.* It gains in rapidity in the morning till 9 o'clock,

and in the evening till 6 o'clock, and falls in the day time, being at its minimum at midnight.

5. Muscular exercise quickens it.
6. It is quicker during inspiration than expiration.
7. It increases with increase of temperature.
8. It is variously affected by emotions.

VELOCITY OF THE BLOOD CURRENT.

The velocity of the blood must not be confounded with the velocity of the pulse wave which bears to it the same relation as the surface waves on a river do to the rate of the stream of water.

It has already been mentioned that the general bed of the blood increases from the aorta to the capillaries, and decreases from the capillaries to the vena cava, on account of the branches or tributaries of nearly every artery or vein being collectively of larger area than the vessel from which they spring or to which they may lead; or, in other words, if we imagined the whole vascular system fused together into one tube it would form two somewhat irregular cones, one corresponding to the arteries and the other to the veins, with their bases placed at the capillaries and their apices at the heart. Between the two a still wider aggregate would represent the capillaries. Compare Fig. 128, p. 231.

Since the same quantity of blood must pass through each section of these cones in a given time, the rate at which it flows must vary greatly in the different parts, being faster in proportion as the diameter of the part is narrower, in accordance with the well-known physical law that with the same amount of liquid flowing its velocity changes inversely with the diameter of the tube. Thus, the mean velocity of the flow in the arteries becomes slower and slower as the capillaries are approached, and in the wide bed of the latter the rate of the current is reduced to a minimum. In the small veins the rate is slower than in the larger trunks, but on the venous side its rapidity never reaches that of the aorta, where it may be said to move at least twice as quickly as in the vena cava.

The following table may be useful in giving a general idea of the average velocity in different parts of the circulation :—

Near valves of aorta—while the ventricles are contracting it reaches	1200 mm. per sec.
Descending aorta	300—600
Carotid	205—357

Radial	100	mm. per sec.
Metatarsal	57	"
Arterioles	50	"
Capillaries	·5	"
Venous radicles	25	"
Small veins on dorsum of hand	50	"
Venæ Cavæ	200	"

In the aorta near the valves the blood current varies in rapidity, because the flow through the aortic orifice is intermittent, and this variation must be more or less communicated to the neigbouring arteries in the form of an increase of rapidity coincident with the beat of the arterial pulse. The variation in the rate of the blood-flow which is caused by the heart-beat diminishes with the force of the pulse as the smaller arteries are approached, and finally ceases completely in the capillaries where under ordinary circumstances the flow is perfectly continuous. In the first part of the aorta the velocity of the blood-flow is reduced to nil after each ventricular beat, while in the capillaries no change is perceived. Between these two extremes all gradations may be found, which follow the same rules as the pulse.

The general mean velocity varies directly with the blood pressure, which bears an inverse relation to the calibre of the arteries, and further, the mean velocity in any one artery, and its branches, will vary with the diameter of the vessels, which are constantly undergoing local changes in size.

Generally speaking, quick heart-beats cause increase in velocity of the stream, but no definite or invariable relation exists between the two, the vasomotor influences having, no doubt, much more effect than the heart-beat on the rate of the stream in the smaller vessels.

In looking at the blood passing through the small vessels of a transparent tissue, such as the frog's tongue or web, it appears that different parts of the column of fluid move with different velocities. Down the centre of the stream the red corpuscles are seen coursing rapidly, while between the central part and the vessel wall on each side a pale line of plasma can be recognised, which seems to flow more slowly and to carry with it only a few white corpuscles.

In the veins the velocity varies enormously with a variety of circumstances which have little or no effect on the arterial flow. Thus, the position of the body or limb, the activity of the neighbouring muscles and the respiratory movements alter it, but as a general rule the flow in the veins is pretty steady, there being no pulsation or corresponding variation of velocity. In the large vessels the onward flow is affected by the contraction of the auricles. During the auricular systole the veins cannot empty themselves, and therefore there is a slight check to the onward flow, and the velocity of the current

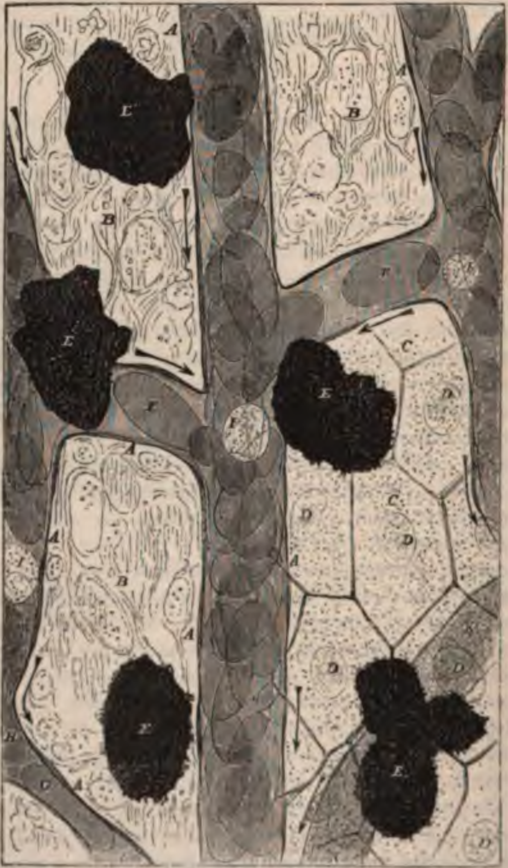


Fig. 142.—Small portion of Frog's Web, very highly magnified. (Huxley.)

A. Wall of capillary vessels.
B. Tissue lying between the capillaries.
C. Epithelial cells of skin, only shown in part of specimen where the surface is in focus.
D. *Nuclei of epithelial* cells.
E. Pigment cells contracted.
F. Red corpuscles (ova in the frog).
G. H. Red corpuscles squeezing their way through a narrow capillary, showing their elasticity.
I. White blood cells.

is accordingly reduced. In cases where the auricles are dilated and distended with blood this may cause a definite pulsation, which becomes visible in the great veins of the neck.

WORK DONE BY THE HEART.

This can only be determined when the mechanism of the vessels is understood. The amount of work done by any form of engine may be expressed as so many kilogrammetres per hour. That is to say, the numbers of kilogrammes it could raise to the height of one metre in that time.

The left ventricle moves with each systole about 0·188 kilogrammes of fluid against an arterial pressure corresponding to 3·20 metres height of blood, *i.e.*, $0{\cdot}188 \times 3{\cdot}21 = 0{\cdot}604$ kilogrammetres for each systole. This at 75 per minute for 24 hours would be—

$$0{\cdot}604 \times 75 \times 60 \times 24 = 65{,}230 \text{ kilogrammetres.}$$

The right ventricle does about one-third as much work as the left, making a total of 86,970 kilogrammetres for the ventricles. Or, in other words, the heart of a man weighing twelve stone does as much work in twenty-four hours as would be required to lift his body 1248 yards into the air, *i.e.*, nearly ten times as high as the top of St. Paul's Cathedral.

CONTROLLING MECHANISMS OF THE BLOOD-VESSELS.

Vaso-Motor Nerves.

That the arteries possessed, as well as elastic resiliency, vital contractibility which regulated the amount of blood flowing to any given part was well known to John Hunter.

The muscle cells have also been long since clearly demonstrated in the middle coats of the arteries, but nothing was known of the nervous channels which bore the stimulus to the vessels, or the nerve centres which regulated their contraction, until comparatively recent times.

The first knowledge concerning special nervous arrangements for the control of the muscular wall of the vessel was given to us by Claude Bernard, in his notable experiment of cutting the sympathetic nerve in the neck, which was always followed by an increase in temperature of that side of the head, and a great expansion and overfilling of the arteries.

It was further observed that stimulation of the superior ganglion of the sympathetic brought about an opposite result, namely, a loss of temperature and contraction of the vessels on the same side as the stimulus was applied. If the stimulus was much increased, the vessels contracted much more than the normal amount, but on cessation of the stimulus they became greatly dilated above the normal point and the temperature rose again, but after a time the effect of the stimulus gradually passed off. From this it was concluded that the sympathetic in the neck conveyed to the muscles in the blood-vessels impulses which caused a certain amount of habitual contraction of the vessel wall, which was called *tonic contraction*, corresponding to what was already recognised as *arterial tone*. When the nerve was divided this tone disappeared, but when gently stimulated it reappeared, and when more strongly stimulated an exaggerated contraction set in causing complete occlusion of many of the vessels.

Subsequent experiments have shown that all the vessels of the body are supplied with similar vaso-motor nerves, section of which destroys their tone, while their stimulation causes contraction of all the vessels in the territory presided over by the stimulated nerve.

Experiment has also shown that these nerves come from the cerebro-spinal axis, passing out from the spinal cord as "communicating nerves," commonly becoming associated with the sympathetic chain, and are distributed to the vessels either as special nerves, branches of the sympathetic (as the splanchnics), or with the general peripheral nerve trunks.

The nerve centre, which governs the vast majority of the vaso-motor channels, lies in the upper part of the medulla oblongata in the floor of the fourth ventricle. This is proved by two facts: 1st, most of the brain may be removed without diminishing the arterial tone; and 2nd, if the spinal cord be cut below the medulla (artificial respiration of course being kept up) the mean blood pressure is found to fall immediately almost to zero, which is due to the relaxation of the smaller arteries consequent on the paralysis of their muscular coat.

The same can be seen in the web of a frog, in which the medulla has been destroyed (pithed) while the circulation is being studied. The small arteries dilate and the pulse becomes apparent in the capillaries, and even in the veins. From these facts it seems highly probable that in the medulla oblongata a *vaso-motor centre* exists, which regulates the contraction of all the vessels, and keeps them constantly more or less contracted; the centre receiving some continuous stimulation, which results in a slight general vascular constriction or arterial tone. The existence of such a centre in the medulla, and of nerve channels in the cord leading from such a centre is made certain by the fact that if a gentle stimulus be applied to a certain part of the medulla, or just below it, simultaneous general vascular constriction sets in and is indicated by a great and sudden rise in the blood pressure.

The action of the vaso-motor centre can be increased, and thereby the tone of the vessels elevated, and the pressure raised, either by (1) direct or (2) reflex excitation. If the blood flowing through the medulla contains too little oxygen or too much carbonic anhydride it stimulates the centre directly and the blood pressure rises. This may be seen by temporarily suspending artificial respiration during an experiment on blood pressure. Reflexly the activity of the vaso-motor centre can be increased by (1) the stimulation of any large sensory nerve, or (2) by sudden emotion (*fear*).

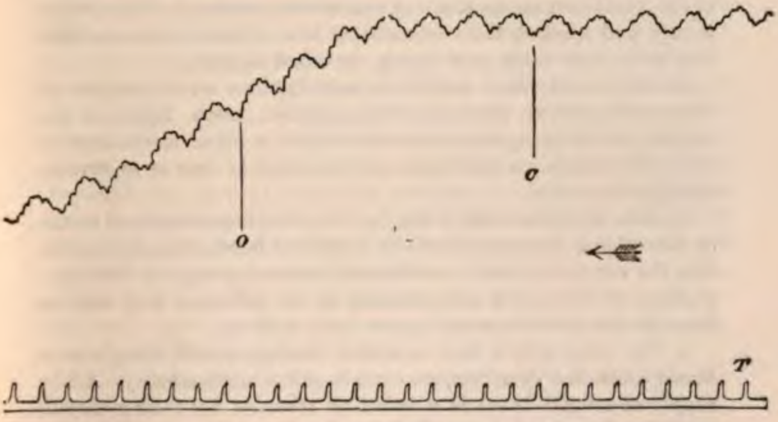


Fig. 143.—Kymographic tracing showing the effect on the blood-pressure curve of stimulating the central end of the depressor nerve in the rabbit. The recording surface moving from left to right. (c) Commencement and (o) cessation of stimulation. There is considerable delay (latency) in both the production and cessation of the effect. (T) Marks the rate at which the recording surface moves, and the line below is the base line. (Foster.)

The tone of the arteries may be diminished by lessening the activity of the vaso-motor centre by the stimulation of a peculiar afferent nerve, the anatomy of which has been made out in the rabbit, and probably has its analogue in man, and which passes from the inner surface of the heart to the medulla. The effect of stimulation of this nerve in lowering the pressure is so great that it has been called the *depressor nerve*. Some emotions (*shame*) may also reduce the activity of the centre, as is seen in blushing, which is simply dilatation of the facial vessels.

Besides this chief vaso-motor centre it is probable that in the higher animals, as certainly is the case in the frog, other centres are distributed throughout the spinal cord which seem to be able to take the place of the great primary centre. For after the spinal cord has been cut high up, the hinder extremities more or less recover their vaso-motor power in a few days, and destruction of the lower part of the spinal cord causes renewed vaso-motor paralysis. In frogs this is very well marked, the centres being less confined to the medulla than is the case in the more highly organised animals.

During recent times numerous investigations on the subject of vaso-motor nerves have, no doubt, thrown much light on the subject, but these inquiries have not made the nerve mechanism by which the various vascular areas are governed so clear or so obvious as might be wished.

In order to explain and reconcile the various experimental truths on this subject (too numerous to be mentioned here), we must suppose that the vaso-motor nerve mechanisms are very complex. The supposition of some such arrangements as the following may help to simplify the matter in some degree to the student.

1. The blood-vessels have muscular elements which, though commonly controlled by nerves, are capable of automatic activity. A free supply of arterial blood is a sufficient stimulus for their moderate action, and mechanical or other stimulus is capable of exciting increased constriction. We know that such automatic contractile elements exist in some of the lower animals (snail's heart, hydra, &c.), and we have no reason to doubt their existence in mammals. Moreover, such a hypothesis obviates the necessity of supposing that local nerve elements exist, which we cannot recognise morphologically.

2. In the medulla oblongata (in close relation to the centres governing the respiratory, cardiac, intestinal, and other movements subservient to the vegetative part of the economy) there exist nerve centres which constantly exert an important influence over the activity of the vessel muscles. These groups of nerve cells called the *vaso-motor centres*, are intimately connected with the centres which preside over the functional activity of various organs and parts, and are also closely related to the nerves coming from all parts of the circulatory apparatus. From these centres impulses of two distinct kinds may emanate, the one increasing the action of the contractile elements, and the other inhibiting it.

3. Direct communication between this *vaso-motor centre* and the contractile elements in the middle coat of the blood-vessels is kept up by means of efferent nerve channels of different sorts, some bearing stimulating (vaso-constrictor) others inhibitory (vaso-dilator) impulses, these being conveyed by nerve fibres which run side by side in the same nerve cord.

4. The activity of the contractile elements of any given vascular area may be altered by impulses arising from different sources. (*a*.) Local influences under ordinary circumstances are brought but little into play, but, if cut off from the nervous centres, are capable of controlling the local blood supply by changing the degree of arterial constriction. (β.) Central influences from the medulla, are habitually in action, affecting all the vessels and keeping up the vascular tone. These impulses are variously modified by changes occurring in distant parts of the circulatory apparatus, and can be regarded as a general regulating mechanism. They probably pass through the sympathetic chain. (γ.) Special influences, which are associated with the functions of the different parts and organs, are only called into operation during the performance of the function, whatever it may be. These impulses probably are conveyed by the same nerves as excite the various forms of functional activity, namely, ordinary peripheral nerves.

These three sets of influences are variously brought about in different parts, and thus we find that section or stimulation of the different nerves gives vaso-motor effects which appear contradictory.

Section of a sensory nerve causes temporary vaso-motor paralysis, owing to the tonic constrictor influence being cut off. Stimulation of the peripheral stump causes vaso-constriction from excitation of the same fibres.

The stimulation of a motor nerve-fibre causes an increase in the flow of blood, or in other words, is associated with a vaso-dilator effect, probably dependent on the inhibitory effect of certain centrifugal fibres which control the local agencies.

Thus we must suppose that there exist local agents under the control of the medullary centres, and that there are two distinct efferent and afferent sets of exciting and inhibitory fibres passing between the centre and periphery, along two perfectly distinct routes; one being in the direct track of the ordinary functional nerve of the part, the other being in the sympathetic, which to a great extent runs along the vessels themselves, and forms most intricate networks capable of carrying impulses in all imaginable directions.

CHAPTER XVIII.

THE MECHANISM OF RESPIRATION.

In its course through the circulation the blood undergoes a series of necessary modifications. The condition of the fluid is thus constantly being altered as it passes from one part and organ to another. It has already been seen that a quantity of nutrient material is taken up by the blood on its way through the capillaries of the alimentary tract. Further, a stream of lymph and chyle is constantly pouring into the great venous trunks, so that from two sources the blood is steadily increased in quantity. But the most urgently essential addition to the circulatory fluid is that which it receives in the capillaries of the lungs. All the blood passes through these organs, in order that the changes taking place in the general systemic capillaries may be counteracted in the lungs. These gas interchanges will form the subject-matter of the present chapter; and the more special modifications which the blood undergoes in the ductless glands, the spleen, the liver, &c., as well as in the kidneys and other excretory glands, will be considered in subsequent chapters.

As has already been pointed out (Chapter V.), an animal during its life may be said to use the substances supplied to it in food as fuel, and thus to acquire the energy which is bound up in them, for the activities of the various tissues are really combustions, being invariably associated with an oxidation of some of the carbon compounds, so as to produce carbon dioxide and water. In order that the structures may undergo this change they must have a ready supply of oxygen constantly at hand, and moreover the carbon dioxide which is formed in the process must be removed, or further combustion would be frustrated. A regular income of oxygen and a regular output of carbon dioxide are then essential to life; hence we find in almost all animals special arrangements by means of which these gases can find their way to and from the tissues and external air respectively. These gas interchanges form the very important function of Respiration.

Here, as in the case of the nutritive materials, the blood acts as the carrier between the tissues and the outer world. The pulmonary half of the circulation is devoted to the gas interchange between the blood and the atmosphere, and is sometimes spoken of as *external respiration.* The gas interchange between the blood and the tissues goes on in the general systemic capillaries, and has therefore been spoken of as the *internal* or *tissue respiration.*

The special arrangement for the taking up of oxygen from the air, and for the giving up of carbonic anhydride to the air is named the pulmonary apparatus. In mammalia this is so far perfected that all the necessary gas interchange can be carried on by the lungs, and the respiratory influence of the external skin or the mucous passages may be regarded as insignificant. But it should be remembered that whenever the blood is in close relation to oxygen, as in the case of swallowed air, the oxygen is soon absorbed by the blood.

In the lower animals the cutaneous surface aids very materially in respiration, and thus frogs can live from this cutaneous respiration alone for an almost indefinite time.

In the lungs the change consists in oxygen being taken from the atmospheric [*] air by the blood and carbonic anhydride being given off from the blood to the air. In the capillaries, on the other hand, the blood takes the carbonic anhydride from the tissues, and yields to them a great portion of its oxygen.

In the lowest class of animals (*e.g.*, amœba) we find no special organs for the purpose of respiration, the gas interchange being sufficiently provided for by the exposure of the general surface of their bodies to the medium in which they live, namely, water.

Other animals have some special apparatus for the purpose of respiration. This apparatus has always the same essential object, that of exposing their tissues to a medium containing oxygen, and of removing the carbonic acid gas.

In some of the invertebrate animals it suffices to distribute the medium containing oxygen throughout the tissues of the animal by means of tubes. Thus in the Echinodermata a water vascular system exists which seems to carry on the function of respiration. A similar distribution of oxygen takes place in arthropoda, delicately branch-

---

[*] The composition of the atmosphere is everywhere remarkably constant, in spite of its oxygen being used up by living beings. It consists of—

Oxygen	21 vols.
Nitrogen	79 ,,
Moisture (variable)	·8 per cent.
Carbonic acid gas (also variable)	·04 ,,

ing open tubes (tracheæ) distribute air to the tissues of the animal's body.

When more active changes occur in the tissues there is always a perfect blood vascular system, and the blood is invariably used as the distributing and collecting agent of the gases in the tissues, and by flowing through some special organ exposed to the surrounding medium it ensures the gas-interchange between the body and the outer world. These organs are formed on two general types: (1) external vascular fringes; and (2) internal vascular sacs.

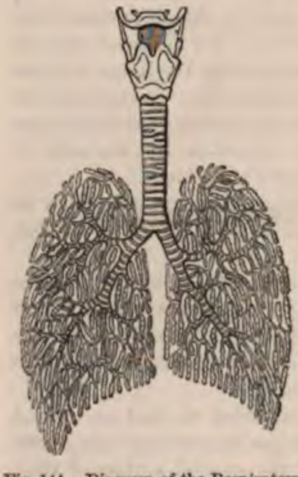


Fig. 144.—Diagram of the Respiratory Organs. The windpipe leading down from the larynx is seen to branch into two large bronchi, which subdivide after they enter their respective lungs.

Animals living in water have commonly the external fringe arrangement (gills) whilst those living in air have sacs (lungs). Some animals (frogs, toads, &c.) have gills in the early stages of their life and lungs when they are more fully developed. In frogs and serpents the lungs are simple sacs, with the inner surface increased by folds of the lining membrane, which gives it a honey-comb appearance; into each sac opens one of the divisions of the air-tube. In crocodiles the air-tubes divide into several branches which open into a series of anfractuous vascular recesses which communicate one with another.

In birds wide bronchial tubes course through the lung tissue to reach large air cavities, and their walls are studded with the openings of innumerable air cells, there being, however, no terminal vascular air cavities as in the mammalian lung.

The respiratory apparatus of mammals consists of (1) vascular sacs filled with air, known as the lung alveoli; (2) channels by which these sacs are ventilated—the air passages; (3) motor arrangements, which carry on the ventilation of the lungs—the thorax.

1. The *lungs* are made up of innumerable minute cavities (alveoli),

with thin septa springing from the inner surface so as to divide the space into several compartments or air-cells. Each of these cavities forms a dilatation on the terminal twig of a branching bronchus, and may be regarded as an elementary lung. The aggregate of these cavities, and the branches of the air passages and vessels distributed to them make up the structure of the lung.

The walls of the cavities are formed chiefly of fine elastic fibres, and the surface is lined with exceptionally delicate and thin celled epithelium. Supported in the delicate frame-work of elastic and connective tissue is the remarkably close-set meshwork of capillaries, in which the blood is exposed to the air. The delicate wall of the vessel, and the thin body of the epithelial lining cell are the only structures interposed between the blood and the air.

2. The *air passages* are kept permanently open during ordinary breathing by the elasticity of more or less rigid tissues. The trachea and bronchi have special cartilaginous springs for the purpose. These are closely attached to the fibro-elastic tissues which complete the general foundation of the walls of the tubes. The air passages are throughout lined with ciliated cylindrical epithelium, which, at the entrance to the infundibula, loses its cilia, and forms but a single layer of flattened cells.

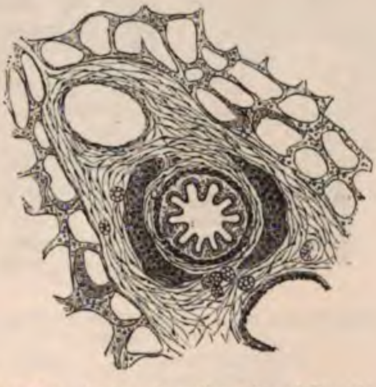


Fig. 145.—Section of small portion of Lung in which are seen a bronchial tube with its plicated lining mucous membrane in the centre, and the large blood-vessels at the sides cut across. Loose areolar tissue and numerous lymphatics surround the large vessels and separate them from the lung tissue.

The air-passages are supplied with muscle tissue of different kinds. Besides the ordinary striated muscles that control the opening of the anterior and posterior nares and pharynx, a special set surrounds the upper part of the larynx, and is capable of completely closing the glottis, and thus shutting off the lung cavities, and proper air passages from the outer air. (V., fig. 144).

In the trachea a special muscle exists which can narrow the wind-

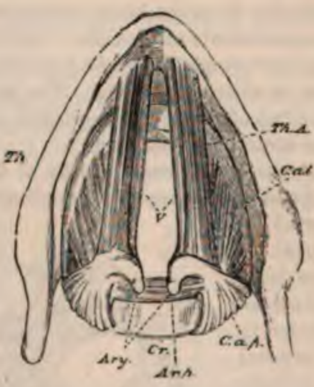


Fig. 146.—Muscles of Larynx, viewed from above.

Th. Thyroid cartilage.
Cr. Cricoid cartilage.
V. Edges of the vocal cords.
Ary. Arytenoid cartilages.
Th.A. Thyro-arytenoid muscle.
c.a.l. Lateral crico-arytenoid muscle.
c.a.p. Posterior crico-arytenoid muscle.
Ar. p. Posterior arytenoid muscle.

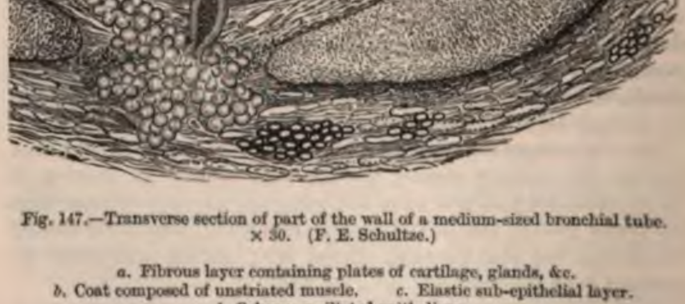


Fig. 147.—Transverse section of part of the wall of a medium-sized bronchial tube. × 30. (F. E. Schultze.)

a. Fibrous layer containing plates of cartilage, glands, &c.
b. Coat composed of unstriated muscle. *c.* Elastic sub-epithelial layer.
d. Columnar ciliated epithelium.

pipe by approximating the extremities of the C-shaped springs that normally preserve its patency.

In the bronchial tubes a large quantity of smooth muscle cells exist, for the most part being arranged as a circular coat, which is best developed in the small tubes (fig. 148, *b*). As we pass from the large to the smaller bronchi the walls become thinner and less rigid, and the cartilaginous plates and fibrous tissue gradually diminish, while on the other hand the muscular and elastic elements become relatively more abundant.

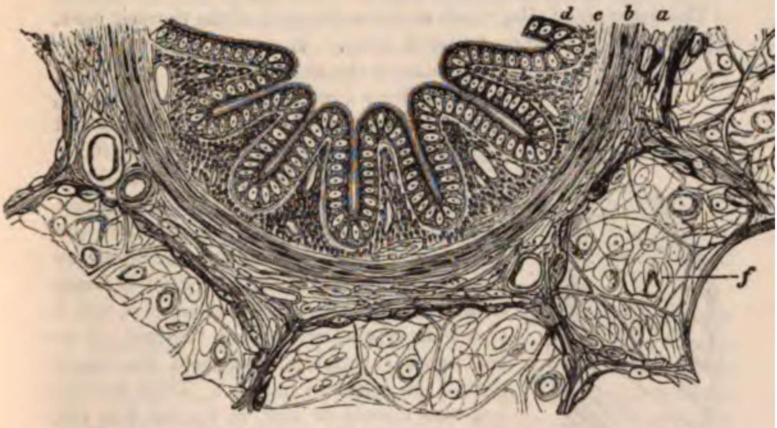


Fig. 148.—Section of a portion of Lung Tissue, showing part of a very small bronchus cut across. (F. E. Schultze.)

a. Fibrous layer containing blood-vessels.
b. Layer of unstriated muscle.
c. Layer of elastic fibres.
d. Ciliated epithelium.

The external surface of the lungs is completely invested by a serous membrane—the pleura, which is reflected to the wall of the thorax from the roots of the lungs, and completely lines the pleural cavity in which they lie. Thus the lungs are only attached to the thorax where the air passages and great vessels enter, the rest of their surface being able to move over the inner surface of the thorax, and to retract from the chest wall if air be admitted into the pleural sac.

3. The *thorax*, in which the lungs are placed, is a bony framework, the dimensions of which can be altered by the muscles which close in and complete the cavity.

The framework is a rounded blunt cone composed of a set of bony hoops—the ribs, attached by joints to a bent pliable pillar—the vertebral column, and held together in front by the sternum, to which they are attached by resilient cartilaginous springs. The ribs slope downwards and forwards, and are more or less twisted on themselves about the middle of the shaft.

The first pair of ribs, which encircles the apex of the thoracic cone, forms part of a short flattened hoop. It slopes downwards in front to reach the sternum. Each succeeding rib from above downwards increases in length, in the amount of its slope downwards and forwards, and in the obliquity of its shaft.

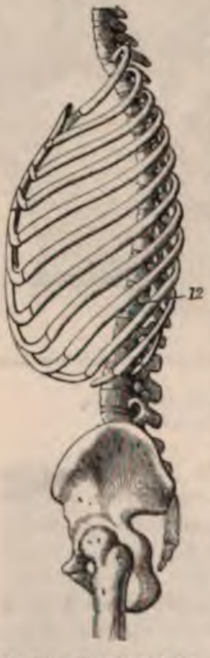


Fig. 149.—Drawing of the lateral view of Thorax in the position of gentle inspiration, showing the downward slope of the ribs.

The floor of the thorax is formed by a dome-shaped muscle—the diaphragm, which bulges with its convex side into the cavity, and separates the thoracic from the abdominal viscera. The upper outlet is closed around the trachea by several muscles, which pass obliquely upwards from the first rib to the cervical vertebræ, and hold the upper part of the thorax in position. These muscles can also elevate as well as fix the first rib, as will be seen when speaking of the muscles in detail. The intervals between the ribs are filled up by two sets of muscle fibres, which cross one another at right angles, and are attached to the margins of the neighbouring ribs.

The base of the thorax is connected by a number of strong muscles with the pelvis and the spine, whence they pass upwards to the lower ribs. The anterior muscles pull down the sternum and anterior part of the ribs. The posterior fix and extend the last rib.

From a mechanical point of view the thorax may be regarded as a specially arranged bellows, the dimensions of which may be increased in all directions.

Within the framework of the bellows is an elastic bag, with the interior of which the outer air communicates by an air-pipe, which is the only passage between the atmosphere and the interior of the bellows. When the framework enlarges its capacity the pressure of the atmosphere pushes a stream of air into the elastic sac, so as to distend it, and thus fill the space caused by the expansion of the frame-work.

By the motions of the framework a stream of air passes in or out of the sac ; a small quantity of the air contained in the lungs is thus changed at each breath, and a certain standard of purity kept up.

In order to fully understand the motions by which the thorax is enlarged, much more detailed knowledge of the anatomy of the bony case and its muscles must be gained than can possibly be given here.

THORACIC MOVEMENTS.

Physiologically the motions are divided into two sets—(1) those which enlarge the thoracic cavity, and cause the air to rush into the lungs, called *inspiration ;* and (2), those which diminish the size of the thorax and force out the air, called *expiration*.

No action of life is more familiar than the rhythmical movements of respiration. The slow quiet rise and fall of the chest and abdomen are the signs most commonly sought as indicative of life ; for every one knows that constant ventilation must go on in order that the blood may readily obtain the necessary amount of oxygen and get rid of the carbonic acid gas, the ordinary diffusion that takes place in the motionless chest being quite insufficient to remove the heavy carbonic acid gas from the lungs.

The rhythm of the respiratory movements may be represented graphically in many ways, by recording either the changes in the diameter or circumference of the thorax, or by the variations of the pressure in the air-passages. These methods more or less correspond, and give curves of somewhat the same character.

The rate of the respiratory movements are up to a certain point under voluntary control, and may be varied by the will, or stopped as when one holds one's breath.

The voluntary control of the respiratory movements is however limited, for if we hold our breath for any length of time, a moment soon arrives when the "necessity of respiration" overcomes the strongest will. The usual respiratory movements are carried on without our being conscious of them, and are, therefore, properly involuntary.

The rate of the respiratory movements varies according to circumstances, being in an adult man about 18 per minute ; in most of the lower animals it is much more rapid. It varies with age, *being very rapid at birth*, decreasing slowly to about 30, and slightly rising towards old age. The following Table (Quetelet) illustrates this :—

A new-born infant	respires	44	times	per minute.
5 years	„	26	„	„
15—20 „	„	20	„	„
20—25 „	„	18·7	„	„
25—30 „	„	16·	„	„
30—60 „	„	18·1	„	„

Muscular exercise increases the rapidity of the respiratory movements, and, consequently, the effort of standing produces a more frequent respiration than is found in the recumbent posture. Emotions variously affect the rate and rhythm of the inspiration and expiration (*e.g.*, sighing); and, finally, morbid conditions, implicating the lungs, usually cause a greater frequency of respiration, sometimes attaining a rate of as many as 60—70 respirations per minute.

The thorax is enlarged in all directions during inspiration, the motion being usually referred to the vertical, tranverse, and antero-posterior diameters respectively.

The vertical diameter is increased by the descent of the lateral parts of the diaphragm, and the slight elevation of the parts about the apex.

The lateral diameter is widened by the side-droop of the ribs being lessened; each rib is rotated upon the line uniting its extremities, and at the same time is moved upward and outward.

The antero-posterior diameter is enlarged by the general elevation of the ribs and sternum, the anterior extremities of the ribs, being drawn up from their general downward incline, push the sternum forwards.

The movements of the diaphragm depress the abdominal viscera lying beneath it, and thereby distend the elastic abdominal wall and compress the gases contained in the intestines. Thus the diaphragmatic movements cause a rhythmical heaving of the abdomen. Respiration depending chiefly on the action of this one muscle is therefore spoken of as *abdominal respiration.* On the other hand, when the ribs are the chief cause of expansion of the upper parts of the chest it is called *thoracic or costal respiration.*

These two types of respiratory movements may be imitated *voluntarily,* and are variously combined in different individuals during *ordinary respiration,* and in the same individual under different *circumstances.*

In men the general character of the ordinary quiet respiration is abdominal, the movement of the thorax being insignificant in comparison with that of the abdomen.

In women the reverse is the case, the abdominal movements are slight when compared with those of the upper part of the thorax. This difference is only well marked during quiet unconscious breathing; any forced or voluntary respiratory effort changes the typical character of man's breathing, and the costal movements become more prominent. In a forced deep inspiration the upper part of the chest shows the greatest increase in the antero-posterior diameter in both sexes.

This difference in type between male and female respiratory movements has been ascribed to different causes. The most common of these is the change brought about by the costume ordinarily adopted by females. This can hardly be an adequate explanation of the phenomenon, for we find the same type existing when the tight garments are removed, and it is apparent in those who have never been constricted by tight clothing, and even in cases where no clothing at all has been used, as amongst the inhabitants of hot countries; so that, though the corset may induce an exaggeration of the costal respiration, by constricting the lower ribs and interfering with the action of the diaphragm, it would not seem sufficiently to account for the normal physiological costal type of breathing found in women.

The occasional distention of the abdomen during pregnancy has also been assigned as a cause of the female type of breathing. That this type of breathing should be transmitted from our female ancestors is possible, but it is very unlikely that pregnancy is the sole agency in producing it, since in childhood the costal type is marked in both sexes. It is probable that the abdominal breathing of the male is also acquired and increased by hereditary transmission, and is really due to the gradual increase in the development of the muscles of the upper extremity in males, causing a greater fixedness of the upper ribs from which they take origin.

INSPIRATORY MUSCLES.

The act of inspiration is not performed by any single muscle; indeed, even the most gentle and quiet respiration requires the co-ordinated action of many sets of muscles. Most of these muscles have other duties to perform besides helping to produce respiratory movements.

Those which are strictly inspiratory in their function are :—

1. The Diaphragm with its accessory Quadratus Lumborum to fix its origin from the last rib.
2. Levatores costarum (including the scaleni) with their accessory intercostals, which act chiefly as regulators.
3. The Serratus porticus superior.

The Diaphragm is the most important inspiratory muscle. It is the only one muscle which unaided can keep up the necessary thoracic ventilation, and, in injury of the spinal cord, owing to its isolated nervous supply, it may be called upon to do so.

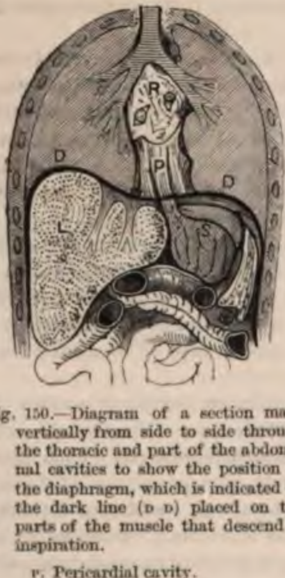


Fig. 150.—Diagram of a section made vertically from side to side through the thoracic and part of the abdominal cavities to show the position of the diaphragm, which is indicated by the dark line (D D) placed on the parts of the muscle that descend in inspiration.

P. Pericardial cavity.
L. Liver.
S. Stomach.
R. Roots of lungs cut through.

During ordinary quiet breathing in the male it does the greater part of the work.

When not in action, a great part of the muscular sheets of the diaphragm lies in direct contact with the inner surface of the lower costal part of the thoracic wall, the rest is higher than the central tendon that forms the floor of the pericardium and is fixed in one position. During inspiration these lateral parts are separated from the ribs and drawn below the level of the central tendon by the contraction of the muscular fibres. The separation is aided by the abduction of the floating ribs, which is accomplished by the quadratus lumborum and the deep dorsal muscles.

In order that the diaphragm may act to the best advantage, it is necessary that its attachments be fixed by the other muscles; for when the quadratus lumborum, levatores and other fixing muscles are not acting, the lower floating ribs are drawn in by the diaphragm, and the power of that muscle is much diminished by the approximation of its attachments. This may be seen in spinal injuries when the respiration is carried on by the diaphragm alone. In these cases a circular furrow marks the line of attachment of the muscle to the lower ribs and their cartilages, which are drawn inwards during each inspiration, the breathing being of course purely abdominal in type.

The *Quadratus Lumborum*, which passes from the pelvis to the last rib has, besides the action in aid of the diaphragm just mentioned, the power of drawing down the lower outlet of the thorax, in which it is helped by other abdominal and dorsal muscles. In this action it may be regarded as the antagonist of the next group.

The *Scaleni muscles*, which pass down from the lateral aspects of the cervical vertebræ to the first two ribs, which they raise so as to draw up the upper outlet of the thorax. The quadratus and scaleni muscles thus act upon the thorax in the same way as the hands when extending a concertina.

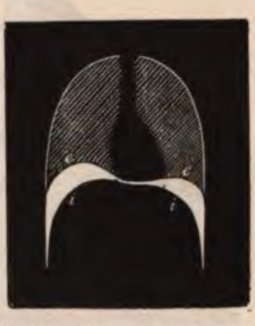


Fig. 151.—Diagram showing interval between the position of the diaphragm in expiration (*e*, *e*) and inspiration (*i*, *i*). The increase in capacity is shown by the white areas.

The *Levatores Costarum* are small muscles, but on account of their number, their aggregate force is much greater than is commonly thought. They are short, thick muscles, which pass obliquely downwards and outwards from the transverse processes of the dorsal vertebræ to the angle of the ribs. Their only action is to raise the angle of the ribs, and thus remove their anterior and lateral downward slopes; by so doing they increase the intervals between the ribs and enlarge the lateral and the antero-posterior diameters of the chest. Thus they are purely muscles of inspiration, and probably, acting with the diaphragm and the scaleni, are the chief workers in ordinary breathing.

The *Intercostals* produce different effects on the ribs according to the different sets of muscles with which they act in association. They never act alone, and it is therefore idle to try to ascribe to them any constant specific inspiratory or expiratory action. Generally speaking, the intercostals approximate the ribs, and by this action they stiffen the thoracic wall and help to elevate the thorax when its upper part is fixed, or, when its lower part is fixed, to depress it.

Now, if both the upper and lower margins of the thorax be held firmly by strong muscles, as really occurs in inspiration—from the action of the quadratus and scaleni—the intercostals cannot approximate the ribs. Under these circumstances the results which follow their contraction will be twofold, viz.:—(1) the sternum will be pushed forwards, and the antero-posterior diameter of the thorax thus increased; and (2) the spaces between the ribs, which are widened by the other muscles, are kept rigid and prevented from sinking inwards when the intra-thoracic pressure falls. When acting with the elevators of the ribs both intercostal layers of muscle have an inspiratory effect. But when the elevators of the ribs are passive the intercostals, acting with the anterior abdominal muscles, draw down the ribs, and act as muscles of expiration.

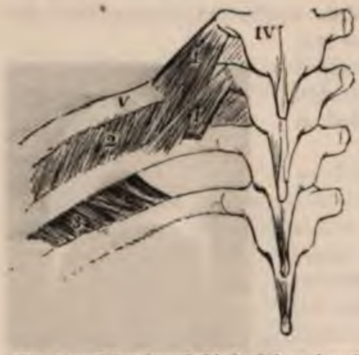


Fig. 152.—View from behind of four dorsal vertebræ and three attached ribs, showing the attachment of the elevator muscles of the ribs and the intercostals. (Allen Thomson.)

1. Long and short elevators.
2. External intercostal.
3. Internal intercostal.

For forced breathing an enormous number of muscles may be called into play during the inspiratory effort, as may be seen during occlusion of the air passages, where all the thoracic, cervical, facial, abdominal muscles, and even the muscles of the extremities, one after another, are thrown into a recurring spasm before suffocation ends the patient's life.

Among the muscles which lend their aid when more energetic inspiratory movements are required, may be mentioned the *sterno-mastoid*, which helps the scaleni to elevate the front of the thoracic wall; the *pectoral* muscles and the *great serratus* which assist when the arms are fixed; and also the deep muscles of the back, which straighten the spine, and act upon the vertebral attachments of the ribs so as to elevate them and widen the intervals between them. Owing to the ribs being fixed to the sternum in front, they can only separate laterally when the dorsal curve is lessened, and this tends to approximate the sternum and the vertebræ, thus narrowing the antero-posterior diameter of the thorax. It is in preventing this flattening of the chest that the intercostals are particularly useful; by holding the ribs together they push forwards the sternum, when the dorsal curve is extended.

During quiet breathing *expiration* requires no muscular effort, the expulsion of the air from the chest being accomplished by the elasticity of the parts.

The most powerful force is the elasticity of the lungs, which are on the stretch even after a forced expiration, and when distended by inspiration are capable of exerting considerable traction on the thoracic wall.

The ordinary shape of the walls of the thorax when the muscles are not acting, corresponds with the position at the end of gentle expiration; therefore the resiliency of the muscles, costal cartilages, and other elastic tissues which are stretched during inspiration tends to restore the ribs to the position of expiration.

The weight of the thorax itself, and the elastic gases in the intestinal tract, which have been compressed by the diaphragm, may also help in expiration.

After death, when the elasticity of the expiratory muscles is lost, the traction exerted by the lungs on the thorax reduces it below the size its own elastic equilibrium would tend to assume; when, therefore, air is admitted to the pleural cavity by puncture, the thorax expands slightly as the lungs shrink, and the pressure on the pleural surface becomes equal to that within the bronchi.

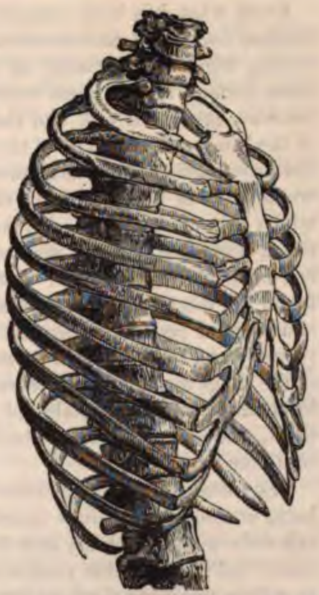


Fig. 153.—Shows the position of the Ribs and the Spinal Column in normal form of the thorax, *i.e.*, that assumed in expiration.

In forced expiration, or when the air is used during expiration for any purpose such as the production of voice, or any blowing movement, a number of muscles are called into action. The only muscles that could be called exclusively special muscles of expiration are the weak *triangularis sterni*, *serratus posticus inferior*, and parts of the intercostals; but in all violent and forcible expiratory efforts these are aided by the muscles forming the anterior wall of the abdomen, which, associated with the intercostals and quadratus lumborum, are the most powerful agents in drawing down the thoracic walls.

Function of the Pleura.

From what has been already said it is obvious that by far the greatest amount of movement takes place in the lower part of the thorax, while the capacity of the apex changes but little. The space formed in the chest during inspiration is practically formed between the costal wall and the diaphragm (compare figs. 148, 149). If the lungs and the walls of the thorax were fused together, without the interposition of serous membranes, the different parts of the lungs would have to follow the movements of that part of the thorax to which they are attached. Thus the lower parts of the lung would be much distended during inspiration, and the apices would receive but little addition to their contained air. This condition is often found in disease of the pleura, leading to adhesion of the visceral and parietal layers. When such cases live for some time after the pleurisy and the adhesions persist, the air cells of the lower margins of the lungs are commonly found to be distended and bloodless (*i.e.*, local emphysema from habitual over-distension); while on the other hand, the apices become abnormally dense, and the alveoli are contracted and airless.

The surface of the soft elastic lung tissue is normally quite free, being encased in a serous membrane, the smooth surface of which can slide uninterruptedly and freely over the similar lining of the costal wall. That this motion of the lung actually occurs may be seen from watching the lung through the exposed parietal pleura, or recognised by studying the sounds produced by a roughness of the pleura, such as occurs in inflammation, when a "friction" can be detected by the ear.

The lungs move in a definite direction. From the most fixed points of the thorax, namely, the apex and vertebral margin, they pass towards the more moveable inferior costal and sternal regions. In short, the anterior part of the lungs passes downwards and forwards to fill up the gap made by the descent of the diaphragm and by the passing of the costal wall upwards and forwards.

The position of the inferior margin of the lung may be easily recognised by percussion over the liver, and may thus be shown to be moving up and down with expiration and inspiration respectively. By percussion we also find that the space between the two lungs in front is increased during expiration and diminished during inspiration, so that the heart is more or less covered by lung, and the præcordial dulness is altered every time we draw a breath.

By means of this free movement of the lungs in the serous cavities the air exerts equal force on the walls of all the air cells whether they are situated in the apex or base of the lung, and the alveoli are all equally filled with air.

If the pleural cavity be brought into contact with the air, either by puncture of the thoracic walls or by rupture of the visceral pleura, the lung, owing to the great elasticity of its tissue, shrinks to very small dimensions, and the pleural cavity becomes filled with air (pneumothorax).

If air be admitted to both pleural cavities so as to produce double pneumothorax, death must ensue, for if the opening remain free the motions of the thorax only alter the quantity of air in the pleural cavity, and cannot ventilate the lungs. This demonstrates the important fact that it is the atmospheric pressure which, having access to them only through the trachea, distends the elastic lungs and keeps them pressed against the wall of the thorax.

The power with which the lungs can contract when the atmospheric pressure is admitted to the pleura has been found after death, without inflation, to be six millimètres of mercury, which is probably below the pressure exerted during life, when the smooth muscle of the bronchi is acting and the tubes are free from mucus, for this rapidly collects in the minute air tubes at death, and impedes the outflow of air.

When the lungs are inflated before the pleura is opened, the pressure can easily be made to rise to nearly 1¼ inches (30 mm. mercury).

From this it would appear probable that when the lungs are stretched by inspiration they exert a negative pressure equal to 30 mm., and when the lungs are in a position of expiration they still tend to contract with a force of 6 mm. mercury.

PRESSURE DIFFERENCES IN THE AIR.

The immediate effect of the increase in capacity of the chest is that a pressure difference is established between the interior of the thoracic cavity and the atmosphere.

The reduction in pressure produced in the lungs and air passages by inspiratory movements, or the increase of pressure accompanying expiration, is very slight during ordinary quiet breathing with free air passages. But the least impediment to the entrance or to the exit of the air at once makes the difference very notable.

It is very difficult to obtain an accurate experimental estimate of the variations in the pressure in different parts of the air passages during quiet breathing, because even the most careful attempt to measure the pressure causes an increase which is still further magnified by the sensitive muscular mechanism of the air passages.

The variations in pressure occurring in the pulmonary air are greatest in the alveoli, and gradually diminish towards the larger air tubes, so that they disappear at the nasal orifice, where, if no impediment be placed to the course of the air, the pressure will remain very nearly equal to that of the atmosphere. By connecting one nostril with a manometer and breathing through the nose with the mouth shut, it can be shown that inspiration causes a negative pressure of about 1 mm. mercury, and expiration a positive pressure of 2 to 3 mm.; these results must be divided by two, since by plugging one nostril they shut off half the normal inlet. Forced inspiration and expiration give respectively −57 and + 87 mm.

This great difference depends on the elastic forces against which the inspiratory muscles act in distending the thorax, all of which assist in expiration.

THE VOLUME OF AIR.

During ordinary respiration the volume of the inspiratory and expiratory stream of air is surprisingly small when compared with the volume of air sojourning in the lungs.

After an ordinary expiratory act we can force out a great quantity of air by a voluntary effort; but even after this is got rid of the lungs are still well filled. Some of this *residual* air, which never leaves the chest during the life of the animal, is pressed out by the elasticity of the lungs when the pleura is opened. But a certain amount of air cannot be removed in any way from the alveoli. Even when the lung is cut out of the chest and divided into pieces, enough air is retained in the air cells, to render it buoyant. This fact is relied on by medical jurists as an evidence that an infant has breathed after birth and distended the lungs with air, for except breathing has been well established, the tolerably fresh lung of an infant will sink in water.

In order to have a clear idea of the volumes of air at rest and in motion during pulmonary ventilation it is convenient to follow the classification from which the nomenclature in common use has been borrowed.

Tidal air is the current of air which passes into and out of the chest in quiet natural breathing. It amounts to about 500 cc. (30 cubic inches).

Reserve air is that volume which can be voluntarily emitted after the end of a normal *tidal* expiration, and which, therefore, during ordinary respiration remains in the lungs; it is estimated at about 1500 cc. (or about 100 cubic inches).

Complemental air is that which can be voluntarily taken in after an ordinary inspiration by a forced inspiration; it also amounts to about 1500 cc., but is not used during ordinary breathing.

Residual air is the air volume which remains in the lungs after a forced expiration, that is to say, which no voluntary effort can remove from the lungs; it includes the air which leaves the lungs when the pleura is opened after death and the air which persistently remains in the lungs after they have collapsed. This amounts to about 2000 cc. (or about 120 cubic inches).

Vital capacity is a term given to the greatest amount of air that can be emitted by a forced expiration immediately following a forced inspiration, so that it equals the sum of the tidal, reserve, and complemental air. The vital capacity is estimated by spirometers of different kinds, and gives an approximate measurement of (1.) The capacity of the chest. (2.) The power of the respiratory muscles. (3.) The resistance offered by the elasticity or rigidity of the walls of the thorax. (4.) The working capacity of the lungs, *i.e.*, their extensibility or freedom from disease. It therefore varies greatly according to the age, sex, position of the body, the occupation, weight, height, the fulness of the hollow viscera of the abdomen, and the pathological condition of the lungs. It can be much increased by practice, and this fact, apart from the injury forced respirations may produce in a morbid state of the lung, renders it inapplicable as a gauge of pulmonary disease.

From the foregoing it appears that the volume of air habitually sojourning in the lungs during natural respiration, or *stationary air*, is about 3500 cc. (225 cubic inches), while the fresh air introduced by each inspiration is only a little over 500 cc. (30 cubic inches), or in other words, about one-seventh of the air in the lungs is changed at each breath. Indeed, the 500 cc. of air is only just sufficient to fill the trachea and larger bronchial passages, so that the fresh air does not reach the pulmonary alveoli, or directly replace any of the air they contain. The tidal stream is, however, brought into immediate relation with the stationary air, and the thoracic movements cause them to mix mechanically, so that rapid *diffusion* takes place in the minute bronchi. Diffusion is also constantly occurring between the air of the small tubes and the terminal sacs, and it alone suffices to maintain the necessary standard of purity in the air of the alveoli. If, during breathing, a harmless gas, such as hydrogen, be inhaled during *one* inspiration, it requires 6 to 10 respirations to get rid of the impurity from the expired air. From this it has been inferred that this number of respiratory acts would be necessary to render the air in the alveoli quite pure even if no fresh impurities were allowed to enter from the blood.

RESPIRATORY SOUNDS.

As the streams of air enter the air passages and lungs they produce sounds which are of the greatest importance to the physician, owing to the manner in which they are altered by disease.

A sound called "bronchial breathing" is produced in the large bronchi and trachea, and is like the noise of air blowing through a tube. This can normally be heard over the trachea, or at the back between the shoulder blades over the entrance of the large bronchi into the root of the lung.

Another sound called "vesicular" can be heard all over the chest, being most distinct where the lung is most superficial, and where other sounds are absent, as in the sub-axillary region. It is a gentle rustling sound caused by the air passing into the infundibuli. It varies much with the force of respiration and many other circumstances. In children up to ten or twelve years of age it is remarkably sharp and loud, and is called "puerile breathing."

NERVOUS MECHANISM OF RESPIRATION.

The movements of respiration go on rhythmically without any voluntary effort, and even when we are quite awake they occur almost without our being conscious of them, and repeated variations take place in the rate, depth, and general type of our respirations without our knowledge. Indeed, if this self-regulating arrangement did not exist we should have to devote much of our attention to adapting our respiratory movements to the ever-changing requirements of the gas-interchange of the blood.

Like all other groups of skeletal muscles, those which act on the thorax are regulated by nerves and work together in harmony. These *co-ordinated* movements are so far under the control of the will that any of the groups of muscles may be employed separately, or in conjunction.

But the respiratory differ from the other skeletal muscles, in that they undergo rhythmical co-ordinated contractions which are not directed by our will, and can be influenced by it only to a certain extent, for they cannot be made to cease altogether.

In short, the rhythmical co-ordinated movements of respiration are not only brought about, but are also regulated by an involuntary nervous mechanism. Since we are unconscious of its action, it certainly is not dependent on the voluntary centres. Moreover, we know that the upper parts of the brain are not needed for regular breathing, because animals born with deficient development of cranium and brain can breathe quite rhythmically ; and removal of the brain of birds &c., causes no interruption of the respiratory movements. We know, however, that an injury to the upper part of the spinal cord causes death by stopping respiration. The regulating *centre* must then be lower than the cerebral centres, and higher than the cervical part of the spinal marrow. The direct evidence of the seat of this centre was found by Flourens, who showed that a localised spot exists in the medulla oblongata, injury of which causes instant cessation of the respiratory movement.

This vital point, or *nœud vital*, is situated in the floor of the fourth ventricle, near the point of the *calamus scriptorius*, and is now commonly spoken of as the respiratory centre.

From this centre the impulses which give rise to and regulate the all-important respiratory movements rhythmically pass down the spinal cord and nerves. So long as the nervous communication between the centre and the muscles is intact the movements go on with undisturbed regularity ; if it be cut off, or the centre destroyed, they instantly stop.

What keeps this centre active ? It has been already stated that all the conditions of the body which cause an increased tissue change, use up a greater amount of oxygen and give off more carbonic acid, therefore are accompanied by more active movements of the respiratory muscles. From this it would appear that there exists some relation between the activity of the respiratory centre and the condition of the blood—a deficiency of oxygen or an excess of carbonic acid gas calling forth increased action. One has only to hold one's breath as long as possible, and note the series of rapid and deep respirations that follow such a temporary impediment to the proper oxygenation of the blood, in order to see that an involuntary respiratory centre is profoundly influenced by a deficiency of oxygen

Experimentally it can be shown that the effect is produced, in a great measure at least, in the medulla itself, by the blood flowing through it, and not by the action of the venous blood circulating through distant organs, and reflexly affecting the centre. It has also been shown that the temperature of the blood circulating through the medulla changes the activity of the centre, for, if the blood in the carotids be warmed, the respiratory movements become more rapid.

The respiratory centre is, then, a good example of what is called an "automatic nerve centre," not depending upon nerve impulses from afar for its energy, nor merely reflecting the influences of other centres, but acquiring its energy from the thermal and chemical condition of the blood which flows through it, and thus its activity is intimately related to its nutrition and supply of oxygen.

So long as the amount of oxygen flowing through the centre keeps up to a certain standard, the normal excitability of the centre continues, and we have natural quiet breathing, called *Eupnœa.* When the oxygen falls below the normal standard, the respiratory centre becomes more excitable, and laboured breathing is produced, commonly called *Dyspnœa.*

If the theory that a deficiency of oxygen is the normal stimulus to action of the respiratory centre be correct, a superabundant quantity should diminish the activity of the centre, and a condition the opposite of dyspnœa would be produced. This is difficult to show in natural breathing, though every one knows the efficiency of the few deep breaths one takes before a dive into water; but with artificial breathing, if the movements be carried on very energetically for some time, and then be stopped, the animal will not at first attempt to breathe, but after a short time, somewhat less than a minute, gentle and slow respiratory movements commence. This cessation of breathing, called *apnœa*, depends upon the blood being so charged with oxygen that it no longer acts as a stimulus to the centre.

We find that dyspnœa is produced by a deficiency in the amount of oxygen rather than by an excess of carbonic acid gas. This is proved by the fact that it occurs when the carbonic acid gas is removed from the blood by breathing freely air which is only deficient in oxygen, and, secondly, because an excess of carbonic acid gas in the air causes a drowsy condition and not an active dyspnœa.

Although the respiratory centre is in the strictest sense *automatic*, yet it is profoundly affected by many influences coming from other *parts*, which reflexly modify the respiratory movements. Thus mental emotions variously influence both the rate and the depth of breathing, sometimes causing more rapid and sometimes slower respiratory action. The application of stimulus to almost any part of the air-passages completely changes the respiratory rhythm. The ordinary sensory nerves passing from the skin are also capable of exciting respiratory movements. This is well seen from the gasping that follows the sudden application of cold to the body. It is along these sensory nerves that one tries to transmit impulses by applying mechanical, thermal, or other stimulus to the skin of a new-born infant, whose respiratory centre having been kept long in the condition of apnœa, is slow to respond to an exciting influence caused by a deficiency of oxygen.

Experiment shows that most, if not all, afferent nerves can affect the respiratory centre, either by increasing or reducing its activity; but there is one special nerve, namely, the *pneumogastric* or *vagus* and its branches, which have both these capabilities developed to a much greater degree than any other.

If the *two* vagi be cut, a marked change takes place in the respiratory rhythm, though section of *one* vagus has little or no effect on respiration. The rate of the inspiration is reduced to less than half, while each breath becomes extremely deep and prolonged, the respiratory function of the lungs goes on for some time unimpaired, and the hæmoglobin of the blood receives the due amount of oxygen. Although the character of the breathing is completely changed from the rapid gentle motion of natural respiration to a series of slow deep gasps, the air volume per minute and the chemical changes remain the same. If the central end of the cut vagus be now stimulated gently, the rate of the respiratory movements may again be quickened to the normal. If the stimulus be very strong, respiratory spasm can be produced. On the other hand, if the central end of the superior laryngeal branch of the vagus be stimulated, breathing becomes slow, and can be made to cease while the thorax is in the position of ordinary expiration, a spasm of the laryngeal and expiratory muscles is caused.

So that in the pneumogastric nerve, fibres exist which convey impulses of two kinds to the respiratory centre, the one increasing its excitability and causing more rapid discharges of inspiratory impulses, the other decreasing its irritability and causing a slowing of the respiratory movements. The marked change which has just been described as occurring when the two pneumogastrics are cut proves that these afferent influences are constantly at work modifying the respiratory rhythm. We may assume that the slow, deep respirations which follow section of the vagi are caused by the un-regulated automatic action of the centre. No impulse is discharged until the

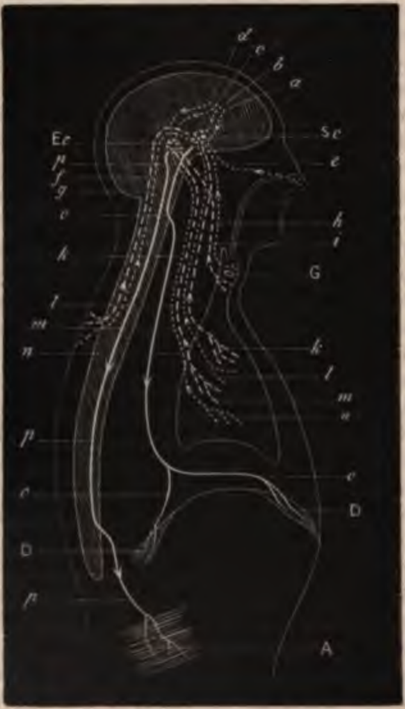


Fig. 154.—Diagram of the Nervous Mechanisms of Respiration. (After Fick.)

Sc. Centre for inspiratory movements, from which pass efferent channels, represented by the continuous white line (*o*) to the inspiratory muscles represented by the diaphragm (D).

Ec. Centre for expiratory movements, from which efferent channels (*p*) pass down the cord to the muscles of expiration, represented by the abdominal muscles (A).

To both these centres *afferent* impulses come (1) from the cerebral centres (*a*, *b*, *c*, *d*) to check or excite activity. These voluntary impulses may be called afferent as far as the respiratory centres are concerned. From (2) the cutaneous surface, and (3) the nose, impulses (*e*, *f*, *g*) arrive, which modify the action of the inspiratory centre. From the (4) larynx (G) come checking impulses (*h*) to the inspiratory, and exciting impulses (*i*) to the expiratory centre. And, finally, (5) from the lungs come both exciting and inhibiting impulses (*k*, *l*, *m*, *n*) to both the expiratory and inspiratory centres, and by these channels the rhythm of ordinary breathing is regulated.

venosity of the blood in the centre arrives at a certain point, and then the accumulated energy is sent to the respiratory muscles, and a eep gasping inspiration occurs, and thus each respiratory act is called forth by the blood becoming so venous as to act as a powerful stimulus.

So long, however, as the centre enjoys the regulating influence of the vagi this venous condition is not allowed to occur, and the intense excitation of the centre is thereby prevented, and the necessary movements performed with a minimum of muscle energy.

The exact mode of stimulation of the pulmonary terminals of the afferent fibres of the pneumogastric is not certain. It has been suggested that distention or retraction of the lungs may act as a mechanical stimulus to fibres inhibiting and exciting respectively the inspiratory centre. Each expansion of the lungs calls forth the ensuing relaxation, and the relaxed state, in its turn, induces a new inspiration, and thus the lungs themselves are able to guide the thoracic movements by means of the pneumogastrics.

MODIFIED MOVEMENTS OF THE RESPIRATORY MUSCLES.

Besides the ordinary respiratory motions and the voluntary modifications made use of in speaking and singing, &c., the muscles of respiration perform a series of movements of an involuntary reflex nature indicative of certain emotions and mental states.

They will be seen to resemble each other in the mechanism of their production, though differing essentially in expression. The following are the more important :—

Coughing is caused by a stimulus applied to certain parts of the air-passages, but more particularly to the larynx ; the stimulus passing along the superior laryngeal branch of the pneumogastric. It consists in a deep inspiration, closure of the glottis, and then a more or less violent expiratory effort, accompanied by two, three, or more sudden openings and closures of the glottis, so that rapidly repeated blasts of air pass through the upper air-passages and mouth, which is generally held open.

Sneezing is caused by a stimulus applied to the nose or eyes, the impulses being carried to the respiratory centre by the nasal and other branches of the 5th nerve. It consists of a deep inspiration and closure of the glottis, followed by a single explosive expiration and sudden opening of the glottis and posterior nares.

Sneezing is a purely reflex act, it being impossible to produce it voluntarily, except by the stimulation of the nasal mucous membrane with some irritating substance.

Laughing consists in a full inspiration, followed by a long series of very short rapid expiratory efforts. The facial muscles are at the same time thrown into a characteristic set of movements.

Crying is made up of a series of short sudden expirations, accompanied with peculiar facial contortions, and commonly following or associated with the following :—

Sobbing, which consists of a rapid series of convulsive inspiratory efforts, causing but little air to enter the chest, and followed by one long expiration.

Sighing is a long slow inspiration, quickly followed by a corresponding expiration.

Yawning is a very long deep inspiration, completely filling the chest. It is accompanied by a peculiar depression of the lower jaw, wide open mouth, facial movements, and commonly stretching of the limbs.

Hiccough is a sudden inspiratory spasm chiefly of the diaphragm, the entrance of the air being suddenly checked by the sudden closure of the glottis.

CHAPTER XIX.

THE CHEMISTRY OF RESPIRATION.

THE simplest way to investigate the study of the gas interchange that takes place in the lungs between the air and the blood is to compare the composition of the expired air with that of the atmosphere, and from the alteration found to have taken place in the tidal stream we can arrive at the changes which the air undergoes during its journey in and out of the air passages, and we can then examine the venous and arterial blood in order to ascertain the change the blood undergoes in becoming arterial.

The atmosphere is made up of a mixture of nitrogen and oxygen, with a variable amount of moisture and a minute proportion of carbonic acid.

The following table gives the *volume** of the gases in dried air :—

Oxygen . . .	20·96 per cent.,	or about 21 per cent.
Nitrogen . .	79·02 „	„ 79 „
Carbonic dioxide	0·02—0·06 „	„ 4 parts in 10,000.

The amount of moisture contained in the air is very variable, and depends in a great measure upon the temperature and the direction of the wind. The dampness of the air depends upon the temperature, so that air containing the same absolute amount of moisture may be relatively dry or damp, according as the temperature rises or falls. As a general rule the air is relatively dry, that is to say, it does not contain so much moisture as it is capable of taking up in the form of aqueous vapour at its ordinary temperature. At certain times of the day the air may be saturated owing to a sudden fall of temperature.

The temperature of the air which we breathe of course varies considerably, according to the season of the year, &c., but almost always in this country it is lower than that of our bodies.

---

* On account of the difference in the atomic weights, the atmosphere being only a *mechanical mixture* of the gases, the proportion by *weight* is slightly different, being about--*Oxygen 23 per cent.*, Nitrogen 77 per cent.

EXPIRED AIR.

The following are the notable characters in the tidal air on its leaving the air passages :—

1. It is rich in CO_2, containing on an average 4·38 per cent. in quiet breathing.

2. It is poor in O, containing about 4·5 per cent. less than the atmosphere.

3. A slight increase in the N. has been observed, possibly the outcome of nitrogenous metabolism.

4. The temperature of the air is approximated to that of the body, and it therefore commonly exceeds the temperature of the air inspired. The air on leaving the air passages is about 36·5° C. This is not much influenced by the temperature of the atmosphere, as may be seen from Valentine's Table :—

Temperatures of Atmosphere		and of Expired Air.
−6·3° C.	=	+29·8° C.
+17·0° C.	=	+36·2° C.
+44·0° C.	=	+38·5° C.

It can be seen from the last statement that very hot air (+44° C.) if breathed is cooled in its transit through the air passages.

5. In quiet breathing the expired air is saturated with moisture ; in rapid breathing this is not the case. It must be remembered that the air when warm is capable of holding a greater quantity of vapour than when it was inspired. The difference can be best appreciated in cold weather, when the vapour of the warm expired air is condensed on meeting the cold atmosphere. Great quantities of water and heat are given off in producing this saturation.

6. If the tidal air be dried and cooled and measured at a certain pressure before and after respiration, it is found that the expired air has lost about $\frac{1}{50}$ of its volume. But owing to the expansion from the increased temperature and the presence of the vapour, the volume of air expired is greater than that inspired.

If the oxygen were all used to make CO_2, these volumes ought to be the same, for the volume of CO_2 is equal to that of the O it contains, if set free. The volume CO_2 given off is, however, only about 4·38, to 4·5 volumes of O taken in, so that part of the O must be used in some other way than in the manufacture of CO_2.

7. *The expired air is also said to contain traces of the following impurities* :—(1) ammonia, (2) hydrogen, (3) carburetted hydrogen

(CH_4), (4) organic matter. These, and probably other impurities, give the breath its peculiar odour and noxious properties, for an atmosphere rendered "stuffy" by expired air is much more injurious to health than an atmosphere in which a similar deficiency of O, or excess of CO_2 had been artificially produced by chemical means; this fact ought to be remembered when calculating the ventilation required for hygienic purposes. The following Table may assist in comparing the atmosphere with the expired air :—

	Atmosphere.	Expired Air.	Difference.
CO_2	·04 per cent.	4·38 per cent.	+4·34
O	20·81 ,,	16·03 ,,	—4·78
N	79·15 ,,	79·55 ,,	+ ·40
Temperature	—6° *C.*— + 35° *C.*	29·8° *C.*—38·5° *C.*	
Moisture	about 10 grms. to 1 cubic metre.	about 40 grms. to 1 cubic metre.	
Volume	....	Apparently increased, absolutely reduced $\frac{1}{40}$th.	
Impurities	....	NH_3, H, CH_4, and poisonous organic matter.	

About $\frac{1}{7}$th of the O which is used does not take part in the production of the CO_2, but this proportion may vary greatly. Thus the estimation of the CO_2 can give no sure guide to the amount of O taken up; and each gas has to be estimated separately if an accurate measurement be required.

The average amount per diem may be said to be :—

Carbon dioxide . . .	given off about	800 grammes.
Oxygen	consumed about	700 ,,
Water	given off about	500 ,,

The amounts of O taken up and of CO_2 given off, differ in different individuals and in the same individuals under varying circumstances, among which the following may be enumerated :—

1. Increase in the rapidity or the depth of respiratory movements, accompanied by an increase in the tidal stream, produces an increase of the total amount of CO_2 given off, while the percentage in the volume of expired air is diminished.

2. It varies with age. The amount increases with age up to 30 years, and then remains constant.

3. Sex; is less in women than in men, but it increases in pregnancy.

4. With muscular activity it is notably increased.

5. Change of temperature of the air has a marked influence on the CO_2 *output of cold-blooded* animals, in which it increases in direct

proportion to the elevation of temperature. The effect on warm-blooded ones is the opposite so long as they can regulate their temperature. The sustentation of the body temperature in cold weather is accompanied by a distinct increase in the output of carbon dioxide.

6. The time of day; a maximum is arrived at about midday and a minimum about midnight.

7. An increase in the amount of carbon dioxide in the atmosphere diminishes the amount given off from the lungs.

CHANGES THE BLOOD UNDERGOES IN THE LUNGS.

In order to understand how the oxygen and the carbonic acid pass to and from the blood in the pulmonary capillaries we must know the relationship of these gases to the blood in the arterial and venous sides of the circulation.

In the chapter on the blood (pp. 193, 194) it is stated that both the oxygen and the carbon dioxide can be removed from the blood by the mercurial air-pump, and that the greater part of these gases are chemically united with some of the constituents of the blood, and that a different quantity of each gas is found in arterial and venous blood. Now that we know that the change from the venous to the arterial condition takes place during the passage of the blood through the pulmonary capillaries where it is exposed to the air, we may assume that the acquisition of oxygen and the loss of CO_2 form the essential difference between venous and arterial blood.

From either kind of blood about 60 volumes per cent. of gas may be extracted with the mercurial gas-pump. The composition of this varies considerably in venous, but not very much in arterial blood. An average is given in the following Table :—

	O per cent. vols.	CO_2 per cent. vols.	N per cent. vols.
Arterial . .	20	39	1—2
Venous . .	8—10 (about)	46	1—2

The more rapidly the gases are removed the greater is the proportion of O that can be obtained; as delay allows some of it to combine with easily oxidised substances in the blood itself. The amount of oxygen varies in different parts of the venous system. In the blood of an animal which has died of slow asphyxia only traces of oxygen can be found.

The proofs that O is, for the most part, in chemical combination with the hæmoglobin of the red blood corpuscles, and not merely absorbed, as one might be led to suppose from its coming away when the pressure is removed, are numerous and satisfactory.

First,—When arterial blood is submitted to gradual diminution of pressure in the mercurial air-pump the oxygen does not come away in accordance with the established law of the absorption of gases (Henry–Dalton) by coming off in proportion to the diminution of the pressure, as at first only traces appear (probably the small amount really dissolved), and when the pressure has been reduced to a certain point the oxygen comes off suddenly ; after which little more can be obtained by further reduction of pressure. Hæmoglobin combines with O in the same way, very rapidly at first when the pressure is low, and then with a much higher pressure a smaller quantity is taken up.

Secondly,—If the oxygen were only in a state of absorption, the blood while passing through the pulmonary capillaries, could only take up about 0·4 volume per cent., which would be inadequate for life. We know that the quantity of O going to the blood from the air in the alveoli cannot well be explained on physical grounds alone ; and, moreover, when an animal is allowed to die of asphyxia in a limited space, all the O of the air in the space is absorbed. Since the partial pressure of the O in this case must fall to zero, it cannot be the pressure which makes the O pass into the blood.

Another conclusive proof that the union of the O with the hæmoglobin is really a chemical one, is given by the spectroscopic examina- of a hæmoglobin solution. When deprived of its O, and after the admixture of the air, quite dissimilar spectra are seen, as already pointed out in Chapter XIV. (Fig. 107).

The amount of O taken up by the blood is not always in proportion to the pressure of that gas, but rather to the amount of hæmoglobin in the blood ; and we therefore find the adequacy of the respiratory function of the blood going hand in hand with its richness in hæmoglobin, and thus the "shortness of breath" of anæmic and chlorotic individuals is explained.

Our knowledge concerning the relation of the CO_2 to the constituents of the blood is less definite and clear.

It does not altogether exist as a mere physical solution, for it comes off irregularly under the air-pump, and does not obey exactly the Henry-Dalton law of the absorption of gases. Part comes off easily and part with difficulty. It is not associated with the corpuscles, for more of this gas can be obtained from serum than from a like quantity of blood. It is more easily removed from the blood than

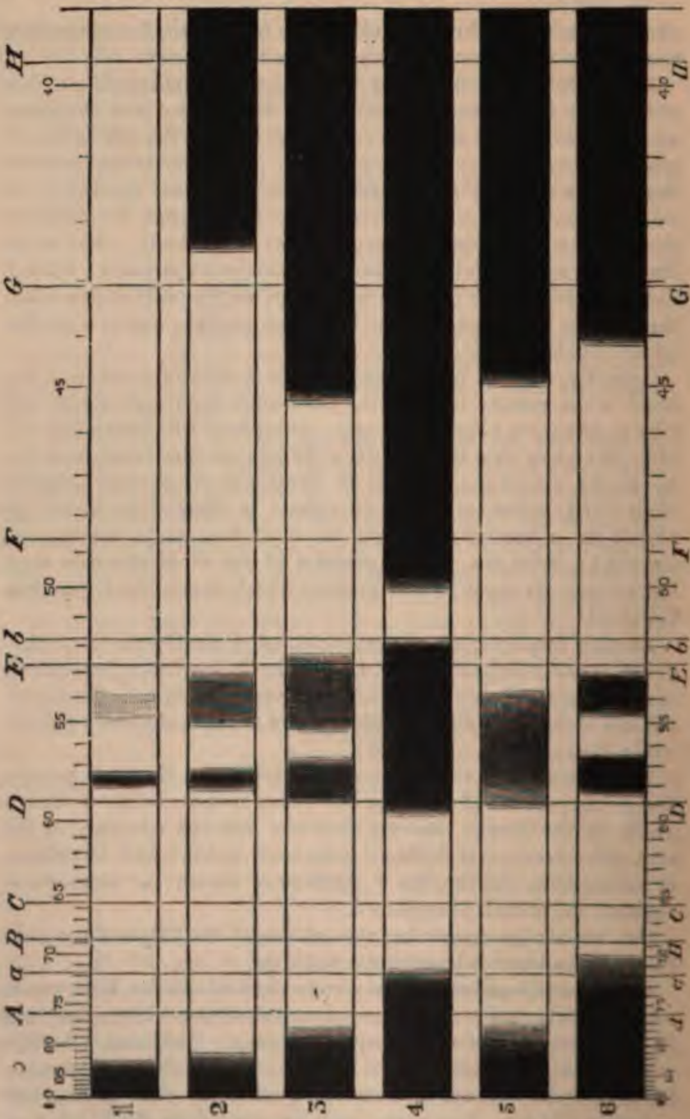


Fig. 155.—The Spectra of Oxyhæmoglobin, reduced hæmoglobin, and CO-hæmoglobi
(Gamgee.)

1, 2, 3, and 4. Oxyhæmoglobin increasing in strength or thickness of solution.
5. Reduced hæmoglobin. 6. CO-hæmoglobin.

from the serum, a certain proportion (about 7 per cent. of the whole) remaining, in the serum in vacuo, until dissociated by the addition of an acid or a piece of clot containing corpuscles. If bicarbonate of soda be added to blood from which all the gas has been removed, still more CO_2 can be pumped out, from which it would appear that something exists in the blood capable of dissociating CO_2 from sodium bicarbonate.

It has been suggested that the CO_2 is in some way associated (possibly as sodium bicarbonate) with the plasma of the blood, and that the corpuscles have the power of acting like a weak acid, and of dissociating it from the soda, and thus raising its tension in the blood.

The great importance of the chemical nature of the union between the O and hæmoglobin for external respiration becomes most striking when the actual manner in which the entrance of the O is effected is taken into account.

It must be remembered that the further we trace the air down the passages, the less will be the percentage of O found in it, and therefore a less pressure exerted by that gas. This is shown by the fact that the air given out by the latter half of a single expiration has less O and more CO_2 than that of the first half. The most impure air lies in the alveoli of the lung, for, since the tidal air scarcely fills the tubes, the air in the alveoli is only changed by mixture and diffusion with the impure air of the small bronchi. Any impediment to the ordinary ventilation of the alveoli so reduces the percentage, and therefore the tension of the O, that it would probably sink below that in the blood, and in that case, were it not a chemical union, the O would escape from the blood in proportion as its tension in the blood exceeded that of the air of the alveoli. We know it does not do this, even in the intense dyspnœa of suffocation.

In the same way the difference of tension of the CO_2 in the alveolar air and in the blood, hardly explains the steady manner in which the CO_2 escapes, and it has therefore been suggested that this escape is also in some way a chemical process, possibly connected with the union of the O and hæmoglobin; because the admission of O to the blood seems to facilitate the exit of the CO_2.

The following table gives the approximate tension of the two gases in the different steps of the interchange, and shows that the tensions are such as to enable physical absorption to take some share in the entrance of the O as well as in the escape of the CO_2. A separate column gives the volumes per cent. of each gas, corresponding to these tensions. This process must occur before the oxygen and the hæmoglobin meet, since the latter is bathed in the plasma, and further separated from the O by the vessel wall and epithelium.

—	CO_2		O	
	Tension in mm. Hg.	Corresponding Volume per cent.	Tension in mm. Hg.	Corresponding volume per cent.
In arterial blood......	21·	2·8	29·6	3·9
In venous blood	41·	5·4	22·	2·9
In air of alveoli	27·	3·56	27·44	3·6
In atmosphere.........	0·38	0·04	158·	20·8

INTERNAL RESPIRATION.

The arterial blood while flowing through the capillaries of the systemic circulation and supplying the tissues with nutriment, undergoes changes which are called internal or tissue respiration, and which may be shortly defined to be the converse of pulmonary or external respiration. In the external respiration the blood is changed from venous to arterial; whereas in internal respiration the blood is again rendered venous.

There can now be no doubt that these chemical changes take place in the tissues themselves, and not in the blood as it flows through the vessels. The amount of oxidation that takes place in the blood itself is indeed very small. The tissues, however, along with the substances for their nutrition, extract a certain part of the O from the blood. In the chemical changes which take place in the tissues, they use up the oxygen, which rapidly disappears, the tension of that gas becoming almost nil; at the same time other chemical changes are indicated by the appearance of CO_2. The disappearance of the O and the manufacture of CO_2 need not exactly correspond in amount, and they doubtless often vary in different parts and under different circumstances. Of the intermediate steps in the tissue chemistry we are ignorant. We do not know the way in which the oxygen is induced by the tissues to leave the hæmoglobin; we can only say that the tissues have a greater affinity for O than the hæmoglobin has, and they at once convert the O into more stable compounds than oxyhæmoglobin, and ultimately manufacture CO_2, which exists in the tissues and fluids of the body at a higher tension than even in the venous blood.

RESPIRATION OF ABNORMAL AIR, &c.

The oxygen income and carbonic acid output are the essential changes *brought about* by respiration, therefore the presence of oxygen in a certain proportion is absolutely necessary for life. The 21 per cent. of O of the atmosphere suffices to saturate the hæmoglobin of the blood, and 14 per cent. of O has been found to be capable of sustaining life without producing any marked change in respiration.

Dyspnœa is produced by an atmosphere containing only 7·5 per cent. of O. This dyspnœa rapidly increases as the percentage of O is further decreased, and when it gets as low as 3 per cent. suffocation speedily ensues.

The output of CO_2 can be accomplished if the lungs be ventilated by any harmless or indifferent gas, and since the manufacture of the CO_2 does not take place in the lungs, its elimination can go on independently of the presence of O in them. The 79 per cent. of N contained in the atmosphere has a passive duty to perform in diluting the O and facilitating the escape of the CO_2 from the lungs.

Indifferent gases are those which produce no unpleasant effect of themselves, but which, in the absence of O, are incapable of sustaining life, such as nitrogen, hydrogen, and CH_4.

Irrespirable gases are such as, owing to the irritating effect on the air passages, cannot be respired in quantity, as they cause instant closure of the glottis. In small quantities they irritate and produce cough, and if persisted in, inflammation of the air passages; among these are chlorine, ammonia, ozone, nitrous, sulphurous, hydrochloric, and hydrofluoric acids.

Poisonous gases are those which can be breathed without much inconvenience, but when brought into union with the blood cause death. Of these there are many varieties. (1.) Those which permanently usurp the place of oxygen with the hæmoglobin, viz.:—carbon monoxide (CO), hydrocyanic acid (HCN). (2.) Narcotic: (a) carbonic dioxide (CO_2), of which 10 per cent. is rapidly fatal, 1·0 per cent. poisonous, and over 0·1 per cent. injurious. (β) nitrogen monoxide (N_2O). Both of these gases lead to a peculiar asphyxia without convulsions. (γ) chloroform, ether, &c.

(3.) Sulphuretted hydrogen (H_2S), which reduces the oxyhæmoglobin, and produces sulphur and water.

(4.) Phosphuretted hydrogen (PH_3), arseniuretted hydrogen ($As\,H_3$), and cyanogen gas (C_2N_2) also have specially poisonous effects.

VENTILATION.

In the open air the effects of respiration on the atmosphere cannot be appreciated, but in enclosed spaces, such as houses, rooms, &c.,

which are occupied by many persons, the air soon becomes appreciably changed by their breathing.

The most important changes are (1) removal of oxygen, (2) increase in carbonic acid, and (3) the appearance of some poisonous materials which, though highly injurious, cannot be determined. The deficiency in oxygen never causes any inconvenience, as it is never reduced below what is sufficient for the saturation of the hæmoglobin. The excess of CO_2 seldom gives any inconvenience, since the air becomes disagreeably fusty or stuffy from breathing long before the amount of CO_2 has reached 0·1 per cent., which amount of pure CO_2 can be inspired without any unpleasantness. It is, then, the exhalations coming from the lungs, and probably skin, some of which must have a poisonous character, that render the proper supply of fresh air imperative.

The difficulty of determining the presence of the poisonous organic materials, makes it convenient to use the amount of CO_2 present in the air as the means of measuring its general purity. We suppose, then, that the relation between the poisonous organic ingredients and the CO_2 is constant.

Air, which is rendered impure by breathing, becomes disagreeable to the sense of smell when the CO_2 has reached the low standard of ·06 or ·08 per cent. That is to say, scarcely twice as much CO_2 as is contained in the pure atmosphere. Supposing that air is unwholesome when its impurities are appreciable by the senses, then, if the animal body be the source of the CO_2, ·06 per cent. of this gas makes the air unfit for use.

An adult man disengages more than half a cubic foot of CO_2 in one hour (·6 Parkes), and consequently in that time he renders quite unfit for use more than 1000 cubic feet of air, by raising the per centage of CO_2 to ·1 (·04 being initial, and ·06 respiratory).

It is obvious that the smaller the space and the more confined, the more rapidly will the air become vitiated by respiration. It becomes necessary for health, therefore, to have not only a certain cubic space and a certain change of air for each individual, but the cubic space and the change of air should bear to each other a certain proportion in order that the air may remain sufficiently pure.

The space allowed in public institutions varies from 500 to 1500 cubic feet per head in such apartments as are occupied by the individuals day and night. As a fair average 1000 cubic feet may be fixed as the necessary space in a perfect hygienic arrangement. In order to keep this perfectly wholesome and free from a stuffy smell, and the CO_2 below ·06 per cent., it is necessary to supply some 2000 cubic feet of air per head per hour.

To give the necessary supply of fresh air without introducing draughts or greatly reducing the temperature of the room is no easy matter, and forms the special study of the hygienic engineer.

Asphyxia.

If the proper supply of oxygen be by any means withheld from the blood so that its percentage is reduced to a certain point, the death of the animal follows in 3 to 5 minutes, accompanied by a series of phenomena, commonly included under the term asphyxia, which may be divided into four stages. 1. Dyspnœa. 2. Convulsion. 3. Exhaustion. 4. Inspiratory spasm.

If the air passages be closed completely the respirations become deep, laboured, and rapid. The respiratory efforts are more and more energetic, and the various supplementary muscles are called into play one after the other, until gradually the second stage is reached in about one minute.

As the struggle for air becomes more severe, the inspiratory muscles lose their power, and the expiratory efforts become more and more marked, until finally the entire body is thrown into a general convulsion in which the traces of a rhythm are hardly apparent. This stage of convulsion is short, the expiratory muscles becoming suddenly relaxed from exhaustion.

Then the longest stage arrives in which the animal lies almost motionless, making some quiet inspiratory attempts. These become gradually deeper and slower, until they are nothing more than deep gasps separated by long irregular intervals.

The pupils of the eyes become widely dilated, the pulse can hardly be felt, and the animal lies apparently dead, when often after a surprisingly long interval one more respiratory gasp follows, and with a gentle tremor the animal stretches itself in a kind of tonic inspiratory spasm, after which it is no longer capable of resuscitation. This last pulseless stage to which the term asphyxia is more properly confined is the most irregular in duration, but always the longest.

The blood of an animal which has died of asphyxia is nearly destitute of oxygen, the hæmoglobin being in a much more reduced condition than is found in venous blood. The first and most obvious effect produced by the circulation of blood so deficient in oxygen is excessive stimulation of the respiratory centre, which causes *the extreme* and varied actions just described. At the same time the venous blood passing through the systemic capillaries affects most profoundly the vaso-motor nerve mechanism, so as to cause a rapid and considerable rise in blood pressure in the first stage of asphyxia. The general constriction of the small arteries may be brought about by the venous blood acting directly as a stimulus to the medullary and spinal vaso-motor centres, to the local centres, or as direct stimulation of the muscle cells of the arterioles themselves. The centres in the medulla which govern the inhibitory fibres of the pneumogastric are also stimulated, and consequently the heart beats more slowly. The increase in arterial tension and the slow beat give rise to distension of the ventricle, which, when a certain point is reached, impedes the working of the heart, and its muscle begins to beat more and more feebly, so that in the third stage the impulse can hardly be felt. The muscular arterioles then become exhausted and relax, the blood pressure falls rapidly, and with the death of the animal reaches zero. Both sides of the heart and great veins are engorged with blood in the last stage of asphyxia; the cardiac muscle being exhausted from want of oxygen, is unable to pump the blood out of the veins, or empty its cavities.

Owing to the force of the *rigor mortis* of the left ventricle, and the greater capacity of the systemic veins, the left side is found comparatively empty some time after death, and at *post mortem* examination the right side alone is found overfilled.

CHAPTER XX.

BLOOD ELABORATING GLANDS.

In the preceding chapters we have seen that the blood undergoes important changes as it courses through the different parts of its circuit. Where it comes in contact with the tissues it yields to them nutrient material for assimilation, and oxygen for their metabolism, and carries away from them some waste products. In the lungs it receives oxygen and gives off carbonic acid. While it flows through the minute vessels of the alimentary tract some of the materials elaborated by the digestion of food are absorbed, and directly added to the blood; at the confluence of the great veins in the neck the stream composed of lymph and chyle is poured into the blood before it enters the heart, so as to be thoroughly mingled with it on its return from the general circulation. Moreover, in various glands, different substances are used in the manufacture of their secretions.

Thus it is obvious that there is a kind of material circulation, a constant income and output going on in the blood itself as it passes through the different parts of the body. The investigation of the exact changes which take place in the blood in each organ or part is surrounded with difficulty, and in many cases it is quite impossible to ascertain what changes occur. In some parts it may be made out by noting the results produced, or the substances given off or taken up by the blood, as seen in the changes found in the air after its exposure to the blood in the lungs, where we can definitely state that the blood has lost or gained certain materials, and is so far altered. In other parts, such as the muscles or the ductless glands, where no doubt profound changes in the blood occur, we have no separate outcome which we can analyse, and we must therefore trust altogether for the elucidation of the change going on in them to the differences which may be found to exist in the blood flowing to, and that flowing from, such an organ. For this purpose one can either *examine samples of the* blood from the artery and vein of the organ, while the ordinary circulation is going on, or, immediately after the removal of the organ, by causing an artificial stream of blood to flow through it; then the changes brought about in the blood by its passage through the organ will give the required information. It can be seen from the foregoing enumeration of processes, that some organs have a double function as regards the blood. Thus, in the lung there is both renovation by taking in oxygen, and purification by getting rid of carbon dioxide. The textures in their internal respiration take the nutriment and oxygen, and give to the blood CO_2 and various other waste products of tissue change.

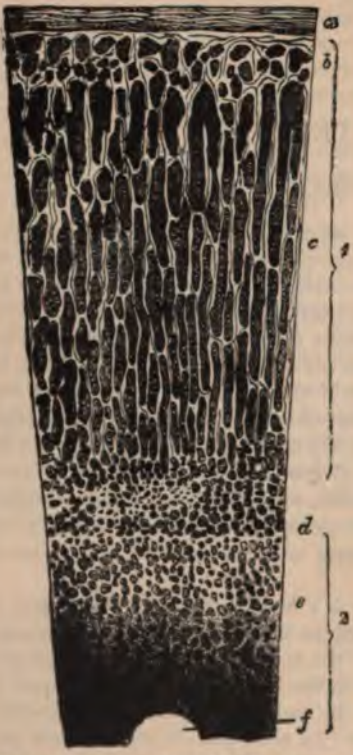


Fig. 156.—Vertical section of the Supra-renal Capsule.

1. Cortex. 2. Medulla.
a. Fibrous capsule.
b. External cell masses.
c. Columnar layer.
d. Internal cell masses.
e. Medullary substance, in which lies a large vein, partly seen in section f.

DUCTLESS GLANDS.

In the preceding chapters the chief sources of income to the blood, viz., the alimentary tract and the lungs, have been considered; and the changes the blood undergoes in its passage through the tissues in the systemic capillaries have been alluded to. The elimination of one of the most important outcomes of tissue change, namely, CO_2, has been described.

It has, further, been shown that a great part of the absorbed nutrient material passes through a special set of vessels called the lacteals or lymphatics, and in so doing has to traverse peculiar organs called lymphatic glands, where it is no doubt modified, and has added to it a number of cells (lymph corpuscles) which subsequently are poured into the large veins with the lymph and become important constituents of the blood.

There is a certain set of organs, which have but slight traits of resemblance to one another, and in consequence of the want of more accurate knowledge as to their exact function, are commonly grouped together as ductless or blood glands. Some of these are doubtless nearly akin to the lymphatic glands, their duty being the further elaboration and perfection of the blood. In this group are commonly placed the supra-renal capsules, the thyroid, the thymus, and the spleen.

SUPRA-RENAL CAPSULE.

With regard to the function of the supra-renal capsule we may say that nothing definite is known. The cortical part is said to resemble the lymph follicles in structure, while the central part, on account of its numerous peculiar large cells, and great richness in nerves, has been explained as belonging to the nervous system.

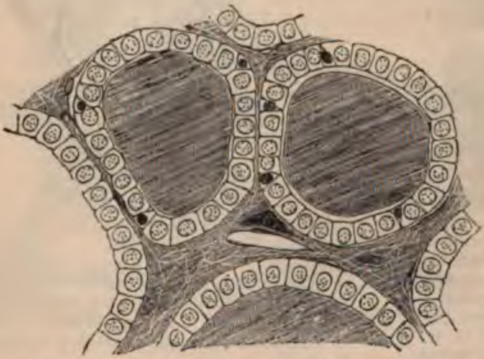


Fig. 157.—Section of the Thyroid Gland of a Child, showing two complete sacs and portions of others. The homogeneous colloid substance is represented as occupying the central part of the cavity of the vesicles, which are lined by even cubical epithelium. (Schäfer.).

THYROID BODY.

The thyroid is made up of groups of minute closed sacs embedded in a stroma of connective tissue, lined with a single row of epithelium cells, and filled with a clear fluid containing mucin. In the adult the sacs are commonly much distended with a colloid substance and peculiar crystals, and the epithelium has disappeared from their walls. Although said to be rich in lymphatics and to contain follicular tissue, positive proof of the relation of the thyroid body to the lymphatic system is still wanting.

THYMUS GLAND.

The functional activity of the thymus is restricted to that period of life when growth takes place most rapidly. It is well developed in the fœtus, and increases in size for a couple of years after birth; but it gradually diminishes in bulk and loses its original structure during the later periods of childhood, so as to become completely degenerated and fatty in the adult. It is composed of numerous little follicles of lymphoid tissue collected into groups or lobules connected to a kind of central stalk. The lymphoid follicles of the young thymus have some likeness to those of the *intestinal tract*, but they differ from these agminate glands not only in

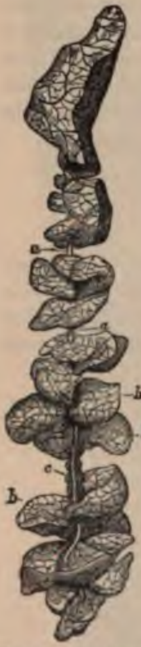


Fig. 158.—Portion of Thymus removed from its envelope and unravelled so as to show the lobules (*b*, *b*) attached to a central band of connective tissue (*a*).

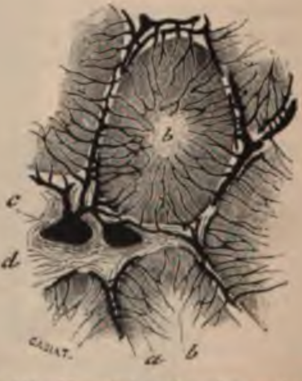


Fig. 159.—Magnified section of a portion of injected Thymus, showing one complete lobule with soft central part (cavity) (*b*), and parts of other lobules. (Cadiat.)

(*a*) Lymphoid tissue. (*c*) Blood vessels.
(*d*) Fibrous tissue.

arrangement but also in having small peculiar nests of large cells (corpuscles of Hassall) in the midst of the adenoid tissue of which they are made up. On account of the structure of the lobules being so nearly identical with that of a lymphatic gland, and from its great richness in lymphatic vessels, the thymus is said to be related to the lymphatic system, and is supposed to play an important part in the elaboration of the blood during the earlier stages of animal life.

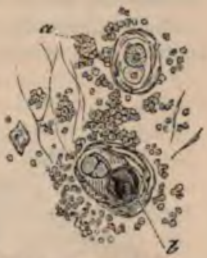


Fig. 160.—Elements of Thymus (high power). (Cadiat.)

(*a*) Lymph corpuscles.
(*b*) Epitheloid nests of Hassall.

SPLEEN.

The spleen also resembles a lymphatic organ in structure, but differs from it in the relation borne by the blood to the elements of the follicular tissue. It is encased in a strong capsule made of fibrous tissue and unstriated muscle cells. From this many branching prolongations pass into the substance of the organ, so as to traverse the soft red spleen pulp. In these trabeculæ or prolongations from the capsule are found the branches of the splenic artery, dividing into smaller twigs without anastomosis. On leaving the trabeculæ the arteries break up suddenly into a brush-like series of small branches, ending in capillaries which are lost in the pulp where the small veins may be seen to commence.

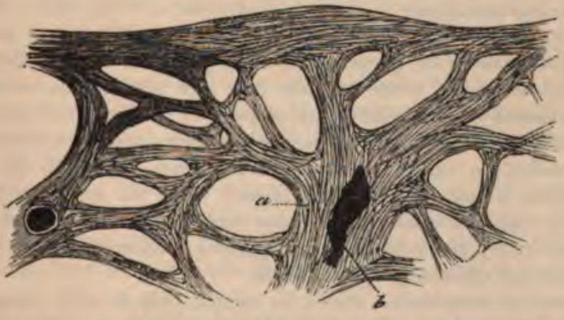


Fig. 161.—(*a*) Trabeculæ of the Spleen. (*b*) Artery cut obliquely. (Cadiat.)

Between the trabeculæ are found two distinct kinds of tissue—(1.) Rounded masses of lymphoid tissue, which are here and there scattered through the organ (Malpighian corpuscles); and (2.) the peculiar soft splenic pulp.

The small rounded masses of lymph follicular tissue are situated on the course of the fine arterial twigs. The delicate adenoid reticulum which holds the lymph cells together, is intimately connected with the vessel wall. The pale appearance of these follicles, which distinguishes them from the surrounding splenic pulp, depends on the number of the white cells which are packed in the meshes of this perivascular adenoid tissue.

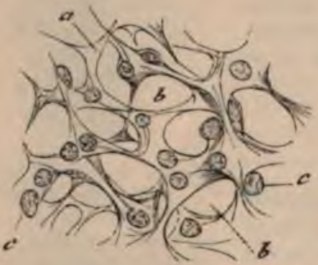


Fig. 162.—Reticulum of the Spleen Pulp injected with colourless gelatine. (Cadiat.)

(*a*) Meshes made of endothelium.
(*b*) Lacunar spaces, through which the blood flows.
(*c*) Nuclei of endothelium.

The splenic pulp consists of a system of communicating lacunar spaces lined with endothelium. Into these spaces the blood is poured from the arteries, and thus mingles with vast numbers of white cells. Besides the ordinary blood discs and the white corpuscles or lymph cells, many peculiar cells are found in the spleen pulp. Some of these look like lymph cells containing little masses of hæmoglobin, and appear to be transitions from the colourless to the red corpuscles, whilst others, small, misshapen, red corpuscles, are regarded as steps in a retrograde change in the discs. But few, if any, lymph channels lead from the spleen-pulp, and only a relatively small number pass out from the hilus, so that the splenic artery and vein must be regarded as taking the place of the afferent and efferent lymph channels.

Chemical examination shows the splenic pulp to have remarkable peculiarities. Although so full of blood, which is generally alkaline, the spleen is acid in reaction, and contains a great quantity of the oxidation products (so-called extractives) commonly found as the result of active tissue change. The chief of these are uric acid, leucin, xanthin, hypoxanthin, inosit, lactic, formic, succinic, acetic, and butyric acids. It also contains numerous pigments, rich in carbon, but little known, which are probably the outcome of destroyed hæmoglobin. A peculiarly suggestive constituent is an albuminous body containing iron. The ash is found to contain a considerable quantity of oxide of iron, to be rich in phosphates and soda, with but small quantities of chlorides and potassium.

If the blood flowing in the artery to the spleen be compared with that in the vein, the difference gives us the changes the blood has undergone in the organ, and hence is of great importance. In the blood of the vein is found an enormous increase in the number of the white corpuscles (1 white to 70 red in the vein, as against 1 to 2,000 in the splenic artery). The red corpuscles from the vein are smaller, brighter, less flattened than those of ordinary blood; they do not form *rouleaux*, and are more capable of resisting the injurious influence of water. The blood of the splenic vein is also said to have a great proportion of water, and to contain an unusual proportion of uric acid and other products of tissue waste.

The amount of blood in the spleen varies greatly at different times. Shortly after meals the organ becomes turgid, and remains enlarged during the later periods of digestion. The size of the spleen, which may be taken as a measure of its blood contents, is also altered by many abnormal conditions of the blood. Thus, in all kinds of fever, particularly ague and typhoid, and in syphilis, the spleen becomes turgid, and in some of these diseases it remains swollen for some time. In a remarkable disease, leucocythæmia, in which the white blood cells are greatly increased in number, and the red ones are comparatively diminished, the spleen, in company with the lymphatic glands, is often found to be profoundly altered and diseased, and commonly immensely enlarged; but, on the other hand, advanced amyloid degeneration of the spleen may occur without any notable alteration taking place in the number or properties of the blood corpuscles.

The spleen may be removed from the body without any marked changes taking place in the blood or the economy generally. It is said that if an animal whose spleen is extirpated be allowed to live for a certain time the lymphatic glands increase in size, or become swollen.

In attempting to assign a definite function to the spleen all the foregoing facts must be carefully reviewed, and the peculiarity of its (1) *structure*, (2) *chemical composition*, (3) the *changes the blood* undergoes while flowing through it, (4) the *variations in blood supply* which follow normal and pathological changes in the economy, and (5) the absence of effect following its *extirpation*, must all be borne in mind.

Its structure teaches us that it is intimately related to lymphatic glands. The Malpighian bodies are simply lymph follicles, and the pulp may be regarded as a sinus like that of a lymph-gland, with this difference, that it is traversed by blood instead of lymph. The cell elements found in it indicate that not only white cells are rapidly generated, but also that these cells have some peculiar relationship to hæmoglobin, as they are often found to contain some. The varieties in size, form, and general appearance of the red corpuscles can be accounted for by either their destruction or their formation occurring in this organ.

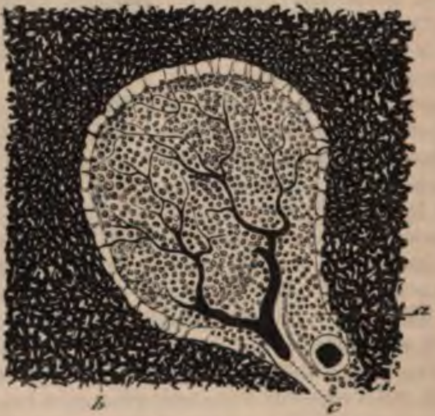


Fig. 163.—Section of Spleen through a lymph follicle (Malpighian body) (*a*) injected to show the vessel; (*c*) entering the follicle, the lymphoid tissue of which is pale in comparison with the pulp (*b*), the meshes of which are filled with injection. (Cadiat.)

Its chemical composition also shows that certain special changes go on in the pulp, and that probably stages of the construction or destruction of hæmoglobin are here accomplished may be inferred from the peculiar association of iron with albuminous bodies.

From the characters of the blood flowing from the spleen it has been argued that, besides an enormous production of white corpuscles, the destruction of the red discs goes on, while some new discs are formed, probably by means of the white cells making hæmoglobin in their protoplasm, which, gradually disappearing, leaves only the red mass of hæmoglobin.

The increased activity of the spleen after meals, and in certain abnormal states of the blood, as shown by its containing more blood, distinctly points out that some form of blood elaboration goes on in it, which is nearly related to, or associated with, nutrition.

The swelling of the lymphatic glands after extirpation of the spleen confirms its relation to these organs, and the fact is undisputed that it is a source of the white corpuscles of the blood; but the paucity of evidence after this operation as to changes in the number or character of the red discs prove that if the spleen be either the place of origin or destruction of the red corpuscles it cannot be the only organ in which they are produced or destroyed.

Glycogenic Function of the Liver.

Of all the organs that modify the composition of the blood as it flows through them, the liver plays the most important part in elaborating the circulating fluid. The elimination of the various constituents of the bile, which has already been mentioned as necessary for the purification of the blood, and useful in aiding absorption, is probably but a secondary function of this great gland. The production of a special material—animal starch—essential to the nutrition and growth of the textures is, in all probability, the main duty of the liver cells, and possibly the constituents of the bile are but the by-products which must be got rid of, resulting from the chemical processes of the manufacture.

In the chapter on the digestive secretions the structure of the liver was mentioned, and attention was directed to the peculiarities of its double blood supply. A relatively small arterial twig takes blood to it from the aorta, while the great portal veins distribute to it all that large supply of blood which flows through the intestinal tract and the spleen.

The blood in the vena porta during digestion can hardly be called venous blood, for much more passes through the intestinal capillaries when digestion is going on than is necessary for the nutrition of the tissue of the intestinal wall. The portal blood is further to be distinguished from ordinary venous blood from the fact that it has just been enriched with a quantity of the soluble materials taken from the intestinal canal, namely, proteids, sugar, salts, and probably some fats; and it has been profoundly modified by the changes taking place in the spleen.

It is from this blood that the liver-cells manufacture the starch-like substance above mentioned. This substance was discovered by Claude Bernard, and called by him *Glycogen*, on account of the great facility with which it is converted into sugar in the presence of certain ferments which exist in the liver itself and in most tissues after death. Shortly after the death of an animal the tissue of the liver, and also the blood contained in the hepatic veins, are extremely rich in sugar, which has been formed by the fermentation of the hepatic glycogen. The quantity of sugar is in proportion to the length of time that has elapsed since the death of the animal, and is minimal, if not nil, if the liver or hepatic blood be taken for examination while the tissue elements are still alive.

The peculiar blood of the great portal vein coming from the stomach, intestines, and the spleen, has then to pass through a second set of capillaries in the liver, and undergoes such important changes that this organ must be regarded as occupying a foremost position among the blood glands. Differences of the utmost importance have long been thought to exist between the blood going to and that coming from the liver, and to it has even been attributed paramount utility as a blood elaborator; but the scientific knowledge of its power in this respect must date from the discovery of its glycogenic function.

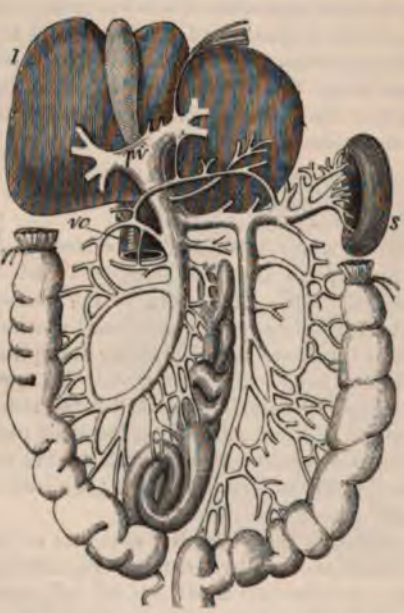


Fig. 164.—Diagram of the Portal Vein (*p v*) arising in the alimentary tract and spleen (*s*), and carrying the blood from these organs to the liver.

Glycogen is a substance nearly allied to starch in its chemical composition, and is converted with great readiness into grape-sugar by the action of certain ferments and acids. Many of the animal textures contain these ferments, among others the liver itself, at least when its tissue is dying; and consequently the liver with the blood coming from it (if examined in an animal some time dead) does not contain glycogen, but sugar which has been formed from it. If a piece of liver taken from an animal immediately after it is killed be plunged into boiling water, so as to check the action of the ferment no trace of sugar is found in it, but only glycogen. After the lapse of a little time another piece of the same liver, which has lain at the ordinary room temperature, will give abundance of sugar.

The mode of preparation of glycogen depends upon the foregoing facts. The perfectly fresh liver taken from an animal killed during digestion is rapidly subdivided in boiling water. When the ferment has been destroyed by heat the pieces of liver are rubbed up to a pulp in a mortar, and then re-boiled in the same fluid. The liquor is then filtered, and from the filtrate the albuminous substances are precipitated with potassio-mercuric iodide and hydrochloric acid, and removed on a filter. From this filtrate the glycogen may be precipitated by alcohol, caught on a filter, washed with æther to remove fat, and dried.

Glycogen thus prepared is a white powder, forming an opalescent solution in water, which becomes clear on the addition of caustic alkalis. It is insoluble in alcohol and æther. With a solution of iodine it gives a wine-red colour, and not blue, like starch, which it otherwise much resembles in chemical relationship.

Glycogen has been found in many other parts besides the liver, namely, in all the tissues of the embryo, and in the muscles, testicles, inflamed organs, and pus of adults; in short, where any very active tissue change or growth is going on, some traces of glycogen can be found.

The amount of glycogen in the liver depends in a great measure on the kind and quantity of food used. It rapidly increases with a full, and decreases with a spare diet, and it slowly falls to nil after prolonged starvation. The formation of glycogen is much more dependent on the carbo-hydrate food than on the proteid, for it rapidly rises with increase in the quantity of sugar taken, and falls, as in starvation, when pure proteid (fibrin) without any carbo-hydrate is used either with or without fat. Although the large supply of glycogen normally manufactured in the liver is probably derived from the sugar of the food, we must not conclude from this that the liver cells cannot make glycogen from other materials. Possibly anything that suffices for the nutrition of their own protoplasm enables the cells to produce glycogen. The slowness with which glycogen disappears in starvation would seem to point to this.

The ultimate destiny and uses of glycogen are still vexed questions.

Much trouble has been taken to decide whether it is converted into sugar, and as such carried off by the blood to the tissues. One set of observers deny the existence in the living tissues of the amylolytic ferment necessary for its conversion into sugar, and think that it is distributed simply as glycogen to the tissues; while others say that it is gradually changed to sugar before it is carried off in the hepatic veins.

The difficulty of determining the exact amount of sugar in the blood with sufficient accuracy may account for the remarkable disparity of opinion on this subject, and makes this a very unsatisfactory means of determining the use or destiny of glycogen. In fact, the whole controversy seems idle, for the real questions are, not whether the glycogen is distributed to the tissues as sugar or not, but is the glycogen distributed to the tissues as a general carbo-hydrate nutritive, or is it to be regarded as a step in the manufacture of some other material by the liver cells; in other words, is the glycogen of the liver a store of special animal carbo-hydrate to be kept till called for, or is it a stage in the formation of fat?

CHAPTER XXI.

SECRETIONS.

THE secretions which are poured into the alimentary tract have been already described in the chapter on digestion. There are other glands which can now be conveniently considered since they more or less alter the blood flowing through them, and thus may be said to aid slightly in the perfect elaboration of that fluid. They are, however, subservient to very different functions; some having merely local offices to perform, and others having duties allotted to them of the greatest general importance to the economy. This becomes obvious from a glance at the following enumeration of the remaining glandular organs.

Secreting glands (other than those forming special digestive juices):—

Lachrymal.
Mucous.
Mammary.
Sebaceous.

Excreting glands:—

Sudorific.
Urinary.

SURFACE GLANDS.

LACHRYMAL GLANDS.

Most vertebrate animals that live in air have a gland in connection with the surface of their eyes, which secretes a thin fluid to moisten the conjunctiva. This fluid commonly passes from the eye into the nasal cavity, and supplies the inspired air with moisture.

The lachrymal fluid is clear and colourless, with a distinctly salty taste and alkaline reaction. It contains only about 1 per cent. of solids, in which can be detected some albumin, mucus, and fat (1 per cent.), epithelium (1 per cent.) as well as sodium chloride and other salts (·8 per cent.).

The secretion is produced continuously in small amount, but is subject to such considerable and sudden increase, that at times it cannot all escape by the nasal duct, but is accumulated in the eyes, until it overflows to the cheek as tears. This excessive secretion may be induced by the application of stimuli to the conjunctiva, the lining membrane of the nose, or the skin of the face, or by strong stimulation of the retina, as when one looks at the sun. A similar increase of secretion follows certain emotional states consequent on grief or joy. These facts show that the secretion of the gland is under nervous control, the impulses stimulating secretion commonly starting either from the periphery, and passing along the sensory branches of the fifth or along the optic nerve, or from the emotional centres in the brain, and arriving at the gland in a reflex manner. The amount of secretion can also be augmented by direct stimulation of the lachrymal nerves, so that in all probability these are the efferent channels for the impulse.

MUCOUS GLANDS..

In connection with mouth and stomach secretions, mention has been made of glands which are elongated saccules lined with refracting cells (Fig. 165). They are distributed over all mucous membranes, and are the chief source of the thick, tenacious, clear, alkaline, and tasteless fluid called mucus.

This material contains about 5 per cent. of solid matters, of which the chief is *mucin*, the characteristic material of mucus, which swells up in water and gives the peculiar tenacity to the fluid. It is precipitated by weak mineral and acetic acids; and, as the precipitate with the latter does not redissolve in an excess, this acid becomes a good test to distinguish it from its chemical allies. Mucin is not precipitated by boiling. Mucus also contains traces of fat and albumin, and inorganic salts, viz., sodium chloride, phosphates and sulphates, and traces of iron.

The fluid is secreted either by the special mucous glands, or it may be produced by the epithelium of the mucous surfaces. The cells produce in their protoplasm a quantity of the secretion, which may often be seen to swell them out to a considerable extent. This clear fluid is then expelled, and the altered cells are repaired or replaced. Many elements, like the remains of epithelial cells, are found in the secretion; and also round nucleated masses of protoplasm similar to white blood corpuscles, after the imbibition of water. In the abnormal secretion of a mucous surface during inflammation these mucous corpuscles are, as well as the general amount of secretion, enormously increased, so that the secretion may become opaque, and may appear to be purulent.

The chief object of the secretion seems to be to protect the mucous surfaces, which are rich in delicate nerves and vessels, and are subjected to many injurious influences of a chemical or mechanical nature. It is analogous to the keratin of the epidermis, and may be regarded as an excretion since it is not absorbed, but is cast out from the mucous passages, and passes from the intestinal tract with the fæces, and from the air passages as sputum, &c.

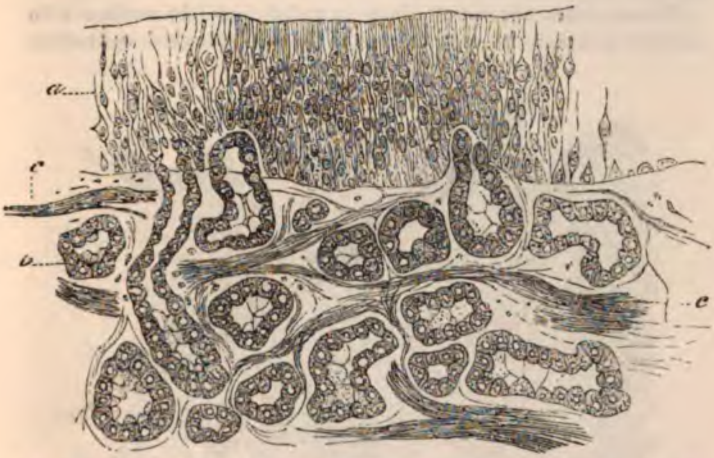


Fig. 165.—Section of the Mucous Membrane of upper part of nasal cavity showing numerous Mucous Glands cut in various directions. *a*, Surface epithelium; *b*, gland saccule; *c*, connective tissue lined with secreting cells. (Cadiat.)

SEBACEOUS GLANDS.

These belong to the outer skin, and commonly open into the follicles of the hairs, but also appear on the free surface of the lips and prepuce, &c., where no hairs exist.

The secretion cannot be collected in great quantity in a normal condition, but as far as can be made out, it is composed of neutral fat, soap, and an albuminous body allied to casein, and organic salts and water, about 60 per cent.

The secretion seems to be made up of the remains of epithelial cells which are thrown off from the inner surface of the glands, while they are undergoing a peculiar kind of fatty degeneration. These cells gradually get quite broken down during their sojourn in the gland alveoli, and the secretion is finally pressed out by the smooth muscle band which commonly embraces the gland and squeezes it against the hair follicle.

This secretion, the use of which is to lubricate the surface with a fatty material, is cast off with the desquamated epithelium

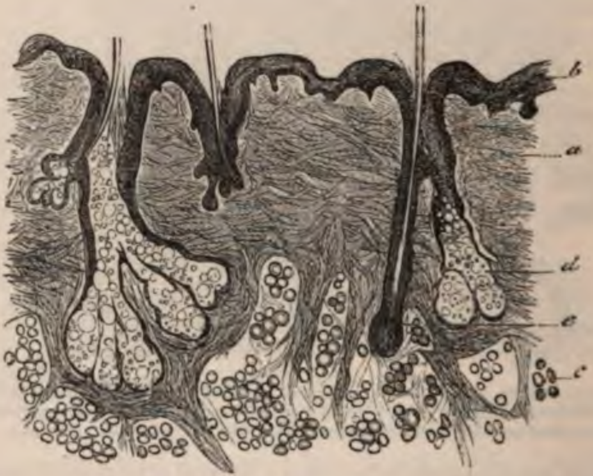


Fig. 166.—Section of Skin showing the roots of three hairs and two large sebaceous glands (d). (Cadiat.)

and the hairs. The Meibomian glands of the eyelids are analogous structures, and are specially elaborated for the lubrication of the ciliary margin. The glands about the prepuce and clitoris are also analogous to the sebaceous glands; in some animals they secrete a peculiarly odoriferous material (Castor).

MAMMARY GLANDS.

The secretion of milk only takes place under certain circumstances, and continues only for a limited period. As the name of the glands implies, they are present in all mammalian animals. The activity of the gland commences in the later stages of pregnancy, and then continues, if the secretion be regularly withdrawn from the gland, for some 9 to 12 months.

During pregnancy the breasts undergo certain preparatory changes prior to the appearance of the milk. They increase in bulk owing to this greater blood supply, and to certain changes in the cell elements of the glands, which are compound saccular glands. Each breast contains a series of some ten to twelve glands with distinct ducts, upon which are dilatations that act as reservoirs in which, during active lactation, the secretion is stored until it is needed.

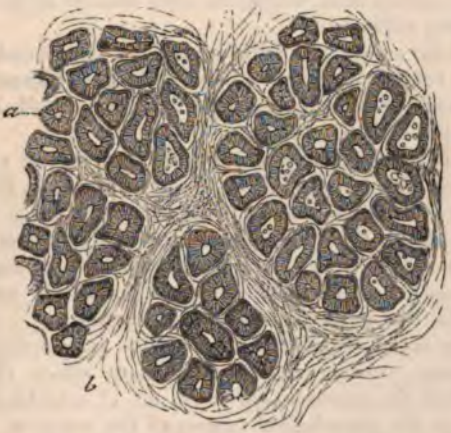


Fig. 167.—Section of Mammary Gland during active lactation (human).

(*a*) Saccules lined with regular epithelium.
(*b*) Connective tissue between the alveoli. (Cadiat.)

The alveoli are chiefly saccular in form, and are lined with a single layer of glandular epithelium, and, during active lactation, contain but little fat, though in the later stages of pregnancy before the secretion is established the cells contain quantities of large fat globules.

Milk is a yellowish-white, perfectly opaque, sweetish fluid, with an alkaline reaction and a specific gravity of about 1030. When exposed to the air, particularly in warm weather, the milk soon loses its alkalinity, first becoming neutral, and then markedly acid; the milk is then said to have "turned sour," but its appearance is not greatly changed. When it has stood a very long time it may crack or curdle, and separate into two parts; one a thick white curd and the other a thin yellowish fluid. This turning sour and ultimate curdling depends upon a change brought about in one of its most important constituents, namely, milk sugar, by means of a process of fermentation. The milk sugar, in the presence of certain forms of bacteria, ferments and gives rise to lactic acid. When the quantity of lactic acid is sufficient, it not only makes the milk sour, but also precipitates another of its important constituents, namely, casein. This albuminous body in its coagulation entangles the fat of the milk, and we have thus formed the curd of cracked milk, whilst the whey consists of the acid, salts, and remaining milk sugar.

Although the curdling of milk depends on the coagulation of an albuminous body, it is never produced by boiling fresh milk, because the chief proteid is casein, a form of derived albumin (alkali-albumin), which does not coagulate by heat.

When milk is preserved from impurities and kept in a cool place, a thick yellow film soon collects on the top of the fluid, the thickness of this layer—the cream, may be taken as a rough gauge of the richness of the milk. For milk consists of a fine emulsion of fat, the suspended particles of which are kept from running together by a superficial coating of dissolved casein. When left at rest, the light fatty particles float to the top and form the cream.

When the mammary glands commence to secrete, the milk contains numerous peculiar structural elements which finally quite disappear from the secretion, but which are of considerable interest in relation to the physiological process of the secretion. These are the colostrum corpuscles, which consist of large spherical masses of fine fat-globules held together by the remains of a gland cell, which encloses the fat-globules as a kind of sac or case, and in which at times a nucleus can be made out.

The most remarkable point about the chemical composition of milk as a secretion is the large proportion of proteid and fat it contains. It appears that there are two distinct albuminous bodies present, viz.: *casein*, which appears identical with alkali-albumin, and another form of albumin allied to *serum-albumin*. The *fats* are present in the shape of globules of various sizes, being in the condition of a perfect emulsion as above stated. They consist of glycerides of palmitic, stearic, and oleic acids.

The milk sugar is very like glucose or grape sugar, but not so soluble. It has the peculiarity of undergoing lactic fermentation.

Of the inorganic constituents of milk the most important are sodium chloride, and phosphates and carbonates of the alkalis; and it is a remarkable fact that the potash compounds, which are the most abundant in the red blood corpuscles, are present in greater quantity than those of soda.

The following table shows the composition of human milk, a comparison of which with that of some domestic animals will be found on page 69 :—

Albumin	39·24	
Fat	26·66	
Milk sugar	43·64	
Salts	1·38	
		110·92
Water		889·08
		1000·00

The relative quantity of the several ingredients of milk varies with the kind of diet used. A vegetable diet increases the per-centage of sugar, but diminishes that of the other constituents, and also the general quantity of milk. A rich meat diet increases both the general quantity and the per-centage of fats and proteids.

The quantity of milk secreted in the twenty-four hours is extremely variable in different individuals, and under different circumstances in the same individual; the average in general being about two pints.

The amount of the different materials in milk varies under the following rules. The proportion of albumin increases as the milk sugar decreases, and the fat remains the same as the period of lactation advances. The portions of milk last drawn are much richer in fats than that which is first taken from the gland. In the evening the milk is richer in fat than in the morning. The general amount of solid constituents falls, up to the age of thirty years, then gains slightly until thirty-five, after which age the milk becomes decidedly thinner. These points should be borne in mind in the selection of a wet-nurse.

Mode of secretion.—Although the blood contains albumins, fats, &c., very similar to those which form the solid parts of the milk, we have good reason for thinking that the constituents of milk are not merely extracted from the blood, but that the manufacture of this highly valuable secretion is due to the activity of the protoplasm of the gland cells, which construct the various ingredients out of their substance.

It has been suggested, as a simple explanation of the formation of milk, that the cells undergo fatty degeneration, and the secretion is then only the debris of the degenerated cells.

Some facts support this view. In the first place the ingredients one finds in milk are suggestive of, though not identical with, the chemical materials which can be obtained from protoplasm by chemical disintegration rather than of any group of substances found in the blood. Further we find that the so-called colostrum corpuscles, which appear to be secreting cells filled with fat particles, are thrown off from the gland in the early stages of the secretion, and appear in numbers in the milk.

But these colostrum corpuscles soon cease to be thrown off in the secretion, and the saccules of the glands during active lactation do not contain any signs of the debris of cast off cells, or any gradations in degeneration. Only one row of finely granular cells is found lining the saccules, and the cavities are filled with globules of various sizes. From this it would appear that in the earlier stages of the production of the secretion, the mammary cells, after a long period of inactivity are so unaccustomed to the duty they are called upon to perform, that they succumb in the effort, and, being unable to produce the rich secretion and retain their vitality, they are cast off. Their offspring, however, after a generation or two acquire the necessary faculty of making within their protoplasm all the necessary ingredients of the milk, and discharge them out into the lumen of the saccules without themselves undergoing any destructive change.

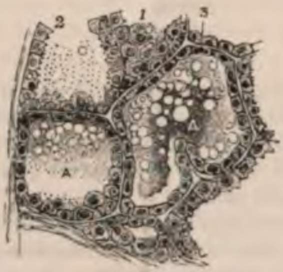


Fig. 168.—Section of the Mammary Gland of a Cat in the early stages of lactation.

(A) Cavity of alveoli filled with granules and globules of fat.

1, 2, 3. Epithelium in various stages of milk formation.

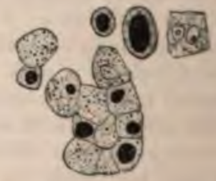


Fig. 169.—Cells of Mammary Gland during lactation, stained with osmic acid, so as to show the various sized oil globules as black masses. (Cadiat.)

The influence of the nervous system on the secretion of the mammary glands is distinctly shown by the wonderful sympathy between the action of these glands and the conditions of the generative apparatus. Further, different emotions have an effect, not only on the quantity, but also on the quality of the secretion. Local stimulation also promotes the secretion, for the application of the child to the breast at once produces this effect, partly, possibly, through mental influences, but chiefly, no doubt, by reflex excitation of the gland following the local stimulation.

For the details of the dietetic value of milk, see Chapter V. on Food, p. 69.

EXCRETIONS.

The term excretion is commonly used to denote a gland-fluid the chief constituents of which are manufactured by other tissues, and are of no use in the economy, but, on the contrary, require to be continually removed in order that their accumulation in the blood may not give rise to injurious consequences. These effete matters are the outcome of the various chemical changes in the tissues whence they are always collected by the blood and carried to the glands which preside over their elimination.

The next form of cutaneous glands are commonly arranged among the excretory organs, though their more important function, as will hereafter appear, is to supply surface moisture for the purpose of regulating the temperature.

SUDORIFEROUS GLANDS.

The *sweat glands* are distributed all over the cutaneous surface, but in some parts, such as the axilla, perineum, &c., they are both more abundant and larger than elsewhere. They are simple tubes extending in a more or less wavy manner through the skin, and ending in a rounded knot formed of several coils of the tube some way beneath the corium, where they are surrounded by a capillary plexus. The tube is lined with glandular epithelium, and its basement membrane is beset with longitudinally arranged smooth muscle fibres.

The *secretion of sweat* is always going on, though it does not constantly appear as a moisture on the surface, because the amount produced is only just equal to the amount of evaporation that takes place. In this case it is spoken of as *insensible* perspiration. Under certain circumstances the sweat collects on the surface and becomes obvious as fluid—*sensible* perspiration—which bathes the skin, being produced more rapidly than it can be evaporated. The quantity of secretion necessary to become sensible varies with the dryness and heat of the air, that is, with the rapidity with which evaporation takes place. It happens, however, that the very circumstances which tend to assist evaporation also promote the secretion of sweat. Indeed, the effect of great heat and dryness of the air is to increase the cutaneous secretion more rapidly than they increase the capability of evaporation, and therefore when the air is hot and dry and evaporation is going on very actively, we have the secretion of sweat made sensible to our feelings. When dampness is associated with warmth of the atmosphere the sweat collects in large quantities on the skin, for the heat, as we shall see hereafter, aids the secretion, and the damp air impedes the evaporation.

The *quantity* of perspiration given off is considerable, but the wide limits within which the amount may vary render an attempt to express an average in numbers useless. The amount will depend on (1) the temperature of the air, (2) the quantity and quality of fluids imbibed, (3) the amount of heat generated in the body, and it therefore varies directly with muscular exercise. The amount that becomes perceptible to our senses depends on the impediments to evaporation that may exist, as well as on the amount of fluid produced.

The *chemical composition* of sweat varies with the amount secreted. When collected as a fluid by enclosing a part of the body in an impervious sac, it is found to have about 2 per cent. of solid matters, the greater quantity of which is made up of inorganic salts, sodium chloride being by far the most abundant. It also contains some epithelial debris, traces of neutral fats, and several volatile and fatty acids (butyric, proprionic, caproic), to which it owes its peculiar smell. It is said to contain urea, but this has been denied, and since all the nitrogenous income is accounted for in the urea excreted by the kidneys, it is probable that the cutaneous elimination of urea is minimal, if not exclusively pathological. It is also said to contain salts of ammonia, and it affords a means of escape to many drugs. In certain parts of the body, especially in some individuals, it contains a considerable amount of pigments, varying in colour from brick red to bluish-black, which need not be here further described.

The *effect of nervous influence* on the secretion of sweat is so associated with the nervous mechanisms of the cutaneous vessels that, under ordinary circumstances, it is a difficult matter to separate them. There can be no doubt, however, that a special nervous control is exerted over the production of sweat. This appears to be observable in some diseases, the poisons of which variously affect the two sets of nerves. Thus, in fever, we observe a dry red skin accompanied by an increased supply of blood, and a suppression of the secretion of the sweat glands; whilst in certain stages of acute rheumatism, the exact opposite is seen, *i.e.*, a profuse sweat drips from the pale bloodless skin. It has, moreover, been recently shown that in some animals (cats) the stimulation of the sciatic nerve, causing contraction of the blood-vessels, produces at the same time a copious secretion of sweat; and a warm atmosphere is said to have no effect on the secretion of a limb the nerve of which has been cut, although the warmth be so great as to make the rest of the animal's body sweat profusely.

The *effect of drugs* upon the cutaneous secretion is well known. There is a large group of medicines, especially pilocarpin, which produce an increased flow, while many others, notably atropin, have a contrary effect.

CUTANEOUS DESQUAMATION.

Together with cutaneous excretion should be mentioned the continuous and extensive loss all over the surface of the body from the casting off of the superficial layers of the dried horny cells of which the outer part of the skin is composed.

The way in which the cells of the mammary gland produce their important secretion is by their protoplasm adopting a peculiar method of fat manufacture, whilst all the strength of its nutritive powers is devoted to the elaboration of the constituents of milk. In a similar way the cells of the epidermis devote their nutritive activity to the production of a certain material—keratin, which cannot be called a secretion in the ordinary acceptation of the term, but which is certainly elaborated as the result of the nutritive changes going on in the protoplasm of the cell during its life-history, just as we know that many other substances are produced as the result of the working of gland cells.

The work of the epidermal cells supplies—not a peculiar chemical re-agent, as do some of the gland cells of the digestive tract, nor yet a nutrient fluid like milk—but the exterior of the body with an insoluble, impervious, tough coating, which though thin and elastic, is very strong and resisting.

The nearest analogy to the secretion of the keratin in the epidermal cells, is the production of mucin in the cells of the epithelial lining of the *mucous membranes*. Both substances may be looked upon as excretions, as they never re-enter the system and are cast off, but each of them performs a definite function, and is produced by special protoplasmic elements, like the secretions more generally recognised as such.

The amount of nitrogenous substances thus excreted cannot well be reckoned, but, having regard to the great extent of surface from which they are derived, it must be considerable.

CHAPTER XXII.

URINARY EXCRETION.

The urine is the most important fluid excretion, for by it, in mammalia, nearly all the nitrogen of the used-up proteid leaves the body in the form of *urea*. The construction of the urinary glands requires the special notice of the physiologist.

Structure of the Kidneys.

The kidneys may be called complex tubular glands, because the tubes of which they are composed are made up of a number of parts essentially differing from one another both in their structure and in their relation to the blood vessels.

The tubes begin by a small rounded dilatation (Malpighian capsule) which is lined by thin flattened epithelium. Opening from this capsule, Fig. 171 (g), is found a tortuous tubule (f), lined by peculiar large rod-beset epithelial cells, which occupy the *greater portion of its*

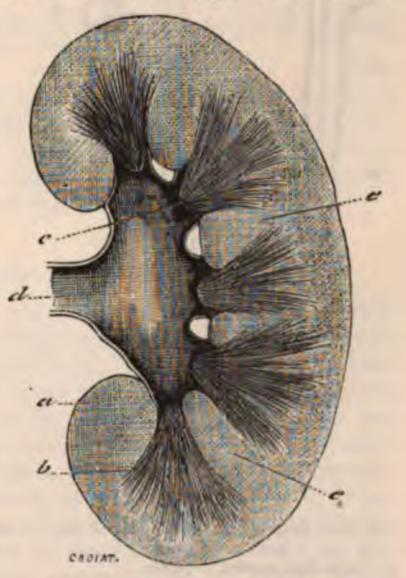


Fig. 170.—Section of Kidney of Man.

a. Cortical substance composed chiefly of convoluted tubules; the portions between the medullary pyramids form the columns of Bertin (e).

b. Pyramids of medullary substance, composed of straight tubes, &c., radiating towards cortex, to form the pyramids of Ferrein.

d. Commencement of ureter leading from central sac or pelvis.

c. Papillæ, where the tubes open into pelvis.—(Cadiat.)

diameter. This convoluted tubule (*f*) leads into a tube (*e*) of much less external diameter, but about equal lumen, owing to the thinness of its lining epithelium, the cells of which are more flattened and much thinner than those in the tortuous tubes. This thin tube *forms a loop* extending down into the medullary pyramid and *returning* to the cortex, where it can be seen to become again con-

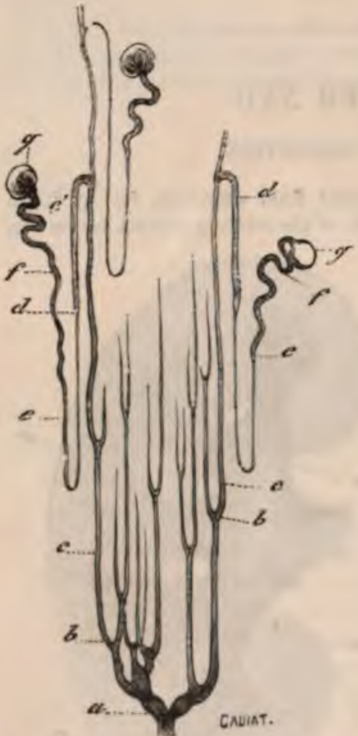


Fig. 171.—Diagram of the Tubules of the Kidney. (Cadiat.)
a. Large duct opening at papilla.
b and *c*. Straight collecting tubes.
d and *e*. Looped tubule of Henle.
f. Convoluted tubules of cortex.
g. Capsule from which the latter spring.

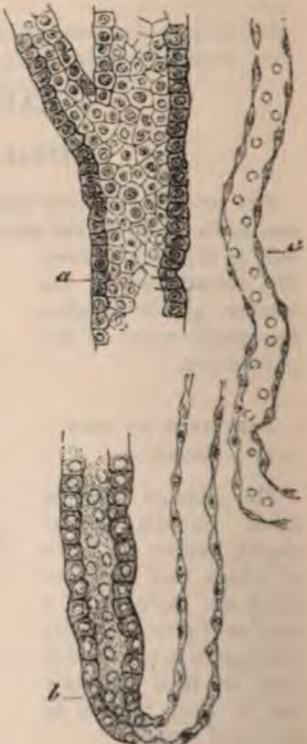


Fig. 172.—Portions of various Tubules highly magnified, showing the relation of the lining epithelium to the wall of the tube. (Cadiat).
a. Large duct near the papilla.
b. Commencement of Henle's loop.
c. Thin part of Henle's loop.

voluted (*d*) and then to open into a straight collecting tube. The collecting tubes (*c*, *b*) receive many similar tributary tubes on their way towards the apex of the Malpighian pyramid, where they pour their contents into the pelvis of the kidney. The epithelial lining of these collecting tubes is of the ordinary cylindrical type.

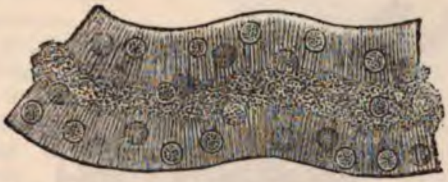


Fig. 173.—Portion of Convoluted Tubule, showing peculiar fibrillated epithelial cells. (Heidenhain.)

We thus find four kinds of epithelial cells in the various parts of the urinary tubules, viz., scaly cells in the capsule; peculiar rod-beset glandular cells in the convoluted tubes; flattened cells in a great part of the loop; and ordinary cylindrical cells in the large straight tubes. (Figs. 172 and 173.)

Blood Vessels.

The renal artery, on its way from the hilus to the boundary between the cortical and medullary portions of the kidney, breaks up suddenly into numerous small branches; these vessels then form arches which run along the base of the pyramids. From the latter, straight branches, called interlobular arteries, pass towards the surface, and give off lateral branchlets which form the afferent vessels to the neighbouring Malpighian capsules. Within the capsules the afferent arteries at once break up into a series of capillary loops, forming a kind of tuft of fine vessels—the *glomerulus*, which fills the cavity at the beginning of the tubules, and is only covered by thin scaly epithelial cells, and thus separated from the urine. It is a singular fact that in the renal circulation the efferent vessel on leaving the glomerulus does not, like most veinlets, unite with others to form a larger vein; but again breaks up into capillaries, which form a dense meshwork around the convoluted tubules. The blood is thence conveyed to small straight veins corresponding to the intralobular arteries.

Another *striking peculiarity* of the renal vessels is that a distinct set of arteries, starting from the same point as the interlobular (between the cortex and medulla), pass towards the centre of the gland into the pyramids. They consist of bunches of straight arterioles, which lie between the straight and the looped tubules. Corresponding with these straight arteries are minute straight veins, which carry the blood back to the vessels at the base of the pyramids.

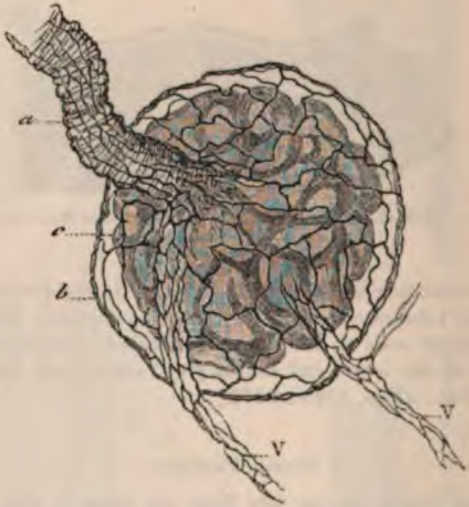


Fig. 174.—Glomerulus, treated with silver nitrate, showing the endothelium.

In the kidney, then, we have three sets of capillary vessels, which differ in their position, the form of their meshes, and their relation to their parent artery. Probably the pressure exerted by the blood in them, and the rapidity of its flow through them, differ also :—

1. The capillaries in the glomeruli are loops collected into a tuft by their covering of delicate epithelium. On account of their relation to the afferent artery which ends abruptly in these capillaries, and to the smaller efferent vessel that leads to a secondary plexus of capillaries, the pressure within the glomerulus must be very great compared with that of the general capillaries of the body, and must vary much with changes in local blood-pressure.

2. The secondary capillary plexus, with its narrow meshwork

closely investing the tubules can only be under comparatively trifling pressure which varies but little, on account of the blood having first to pass through the capillaries of the glomerulus. Their current of blood must also move slowly, since the bed of the stream is here very great.

3. The straight vessels, with long meshed capillaries, in the pyramids between the looped and straight tubules are unlike the two preceding. In these straight vessels the blood probably flows with greater velocity than in those around the convoluted tubes; and their blood-pressure is less than that in the glomeruli but greater than that in the intertubular capillaries.

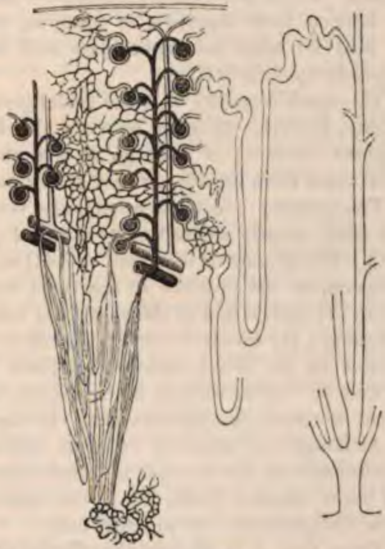


Fig. 175.—Diagram showing the relation borne by the blood vessels to the tubules of the kidney. The upper half corresponds to the cortical, the lower to the medullary part of the organ. The plain tubes are shown separately on the right, and the vessels on the left. The darkly shaded arteries send off straight branches to the pyramid and larger interlobular branches to the glomeruli, the efferent vessels of which form the plexus around the convoluted tubes.

THE URINE.

When freshly voided the urine of man in health is a clear straw-coloured fluid, with a peculiar aromatic odour. The intensity of the colour varies with the amount of solids—the colour being a rough indication of the degree of concentration. On standing and cooling a slight cloud of mucus often appears floating in the fluid. This comes from the lining membrane of the bladder, and it usually entangles a few flattened epithelial cells, which are the only organised structural elements found in it in health.

The fresh urine has a distinctly acid reaction. This does not depend *upon the* presence of free acid, as is suggested by the fact that no precipitate is formed on the addition of sodium hyposulphite, but upon the large amount of acid salts, particularly acid sodium phosphate, which it invariably contains. A strictly vegetable diet renders man's urine alkaline, and it is said to become less acid after meals. In the herbivorous mammalia the urine is normally alkaline so long as their digestion is going on, but when they are deprived of food for some time it becomes acid, showing that the alkalinity depends upon their diet.

The specific gravity of urine varies greatly at different times, commonly, however, ranging between the figures 1015—1020. After copious drinking it may go as low as 1003, and after prolonged abstinence from liquids, or very active sweating, it may attain 1040.

The quantity of urine secreted is also very variable, that produced by an adult usually amounting to about 2 pints per diem (1000—1500 c.c.). The amount is increased by—(1) elevation of the general blood-pressure, or the pressure in the renal vessels from any cause whatever; (2) contraction of the cutaneous vessels from cold; (3) copious drinking; (4) excess of nitrogenous diet; (5) the presence of soluble matter in the blood, such as sugar, salt, &c.; and, (6), the presence of urea as well as various medicaments, has a special action on the renal secretion, greatly increasing the amount of urine passed.

Although the quantity of urine differs so much under different circumstances, the amount of solids excreted by the kidneys in the 24 hours remains pretty much the same, being on an average over 1½oz. (50 grammes) for an adult man.

From this it is obvious that the height of the sp. gr. must vary inversely with the amount secreted, so that the more scanty the urine the higher we expect to find the per-centage of solids.

SECRETION OF THE URINE.

We have just seen that the arterial twig, or *afferent vessel*, which enters the capsule of Malpighi, breaks up into a set of capillary loops, which are only covered by a single layer of extremely thin epithelial cells separating them from the lumen of the urinary tubule, and that the pressure in the vessels of the glomerulus is habitually higher than that in most capillaries, and constantly greater than that of the second capillary network around the convoluted tubules.

The general arrangement of these vessels, and the high pressure in the glomerulus, give the impression that it is simply a filtering apparatus by means of which the fluid parts of the blood pass into the urinary tubules. This view seems supported by the fact that the quantity of urine secreted bears a direct proportion to the blood-pressure in the minute renal vessels, whether the change in pressure depends on local vascular mechanisms or on changes in the general blood-pressure.

Such a theory, however, cannot adequately explain the formation of urine, because the urine differs so materially from the fluid one could obtain as a filtrate from the blood. In health it contains no albumin, a substance in which the blood is very rich ; and it has enormously more urea and salts than the blood. There is, therefore, both a quantitative and qualitative difference, which implies a distinct process of selection, and although filtration cannot be altogether excluded from the process, it must be completely modified by other forces.

Moreover, in the general description of the organ we have just seen that in a great part of the tubules, both the epithelial and vascular supply give the idea of actively secreting gland tubes. From the mere construction of the different portions of the gland it has been concluded that there are two distinct departments each of which play a different part in the production of the urine. One is a simple filtering mechanism, and the other a definitely secreting glandular tubule.

It is not surprising that, with such a complex arrangement as the tubules above mentioned, there should exist different views as to the exact mode in which the urine is secreted. As these are more or less at variance in their explanation of the method of secretion, and as it is difficult to put any of them aside as quite erroneous, it becomes necessary to enumerate each somewhat in detail.

Feeling convinced of the filter-like function of the glomerulus, and recognising the fact that some other agency was also at work in the formation of urine, Bowman explained the process thus :—From the glomerulus the watery parts of the fluid are filtered, while the glandular epithelium selects the important solid constituents which it is necessary to remove from the blood.

Ludwig takes a different view. He believes that the watery part of the plasma, bearing with it the salts, &c., is filtered from the glomerulus. As this fluid passes through the tortuous urinary tubules, a large portion of the water is re-absorbed into the capillary networks surrounding them. This re-absorption is assisted by the high specific gravity of the blood and the low pressure in these capillaries as compared with the glomeruli, where the filtration of the liquid occurs. The *rôle* of the epithelium is not then selection from the blood of specific materials, but possibly the prevention of the return of the solids with the water back to the blood vessels.

Heidenhain attempted to settle the question as to the function of the renal epithelium, by introducing into the blood a blue colouring matter—pure sodium sulphindigotate—which he found to be eliminated by the kidneys, giving rise to blue urine. On examining the organ with the microscope at a suitable time after the injection of the colour into the blood, the tubules are found to be filled with the pigment, and in some cases the peculiar epithelium of the convoluted tubules is stained with the blue substance, while the glomerulus and capsule are entirely free from the colour. If the stream of fluid from the glomerulus be stopped in any way—tying the ureter, section of the spinal cord, or local destruction of the glomeruli—the blue colour is only to be found in the convoluted tubes and their epithelium, and hence it has been concluded that its presence in the looped and collecting tubes of the kidneys and urinary bladder, depends upon its being washed out of the convoluted tubes by the stream of fluid filtered from the blood at the glomerulus.

The following facts may also be adduced in further support of the view that the glandular epithelium bears no mean share in the removal of the more important solid constituents of the urine.

The epithelium in the tubules of the kidney of birds is found impregnated with acid urate of potassium, which insoluble substance forms the chief constituent of the solid urine of birds.

The amount of liquid passing out at the kidneys is in direct proportion to the blood pressure, whereas the excretion of the specific constituents of urine is independent of the pressure, but is related to the amount existing in the blood, and the condition of the epithelium. This is shown by the increased elimination of urea when that substance is artificially introduced into the circulation, even after the flow of the fluid has been checked by section of the spinal cord.

Another view has been put forward, which, with some modification, appears plausible, or at least worthy of mention. Paying attention to the fact that where vascular filtration—*i.e.*, the passage of liquid under pressure through the capillary wall—occurs elsewhere in the body it is not only water and salts, but plasma that passes out of the vessels into the interstices of the tissues, we may then assume that the fluid part of the blood, as such, and not merely its watery part, escapes at the glomerulus. That is to say, the solid ingredients of the urine in a diluted form, plus serum-albumin, pass into the tubules. But on its way down the long and circuitous route through the tubules the albumin with much water is reabsorbed by the *capillaries of the* convoluted tubes. The first step in this case is a *mechanical filtration*; the second is a vital process of re-absorption of a solution of serum-albumin carried on by the gland cells in the tubules, aided by the low pressure in the peri-tubular capillary plexus. This view seems supported by pathological experience, which teaches that the removal of the epithelium of the tubes (the glomeruli remaining perfect), is followed by the appearance of albumin in the urine, and cysts formed by the destruction of the epithelium and occlusion of the tubules commonly contain a fluid somewhat like plasma.

Doubtless much remains to be found out as to the exact method of secretion of the urine, and possibly future research may show us that all the views here enumerated have some truth in them. That a filtration, not mere osmosis, takes place, is made certain by the special vascular mechanism of the glomerulus. Why simply water and salts without albumin should pass through the capillaries of the glomerulus, and not through any other capillaries, is not sufficiently explained to make it sure that this filtration differs from others. That the glandular epithelium does take an active part in the elimination of the urea is rendered almost indisputable from the researches of Heidenhain. And yet there remain other parts, *e.g.*, the loops of Henle, which are constantly found in the kidney, and have a special vascular mechanism, and to which none of the foregoing theories assign any special or peculiar function.

From the foregoing evidence we may fairly suppose that most of the urea, and possibly some other solid constituents of the urine, are selected from the blood by the epithelial cells of the convoluted tubules, that the fluid part of the blood escapes at the glomerulus, and flows along the varied and circuitous route of the tubules, carrying with it the matters poured into the tubes by the cells, and that in some part of the tubules the dilute filtrate loses much of its water and all its albumin.

CHEMICAL COMPOSITION OF URINE.

The per-centage of the various materials in urine varies as the secretion differs in strength, as mentioned, but on an average it may be said to contain about 4 per cent. of solids and 96 per cent. water.

The following are the more important solid matters :—

Urea is the most important, and at the same time most abundant solid constituent, commonly forming about 2 per cent. of the urine. It is regarded as the chief end-product of the oxidation of the nitrogenous matter in the body, so that the amount excreted per diem gives us the best estimate of the amount of chemical change taking *place in the tissues.* It is readily soluble in alcohol and water, but insoluble in ether. It forms acicular crystals with a silky lustre. From a chemical point of view it may be regarded as the diamide of carbonic acid, with the formula $CO\left\{\begin{matrix}NH_2\\NH_2\end{matrix}\right.$, or $\left.\begin{matrix}O\\H_2\\H_2\end{matrix}\right\}N_2$. It is isomeric with ammonium cyanate $\left.\begin{matrix}CN\\NH_4\end{matrix}\right\}O$, from which it was first prepared artificially. It is also isomeric with the amide of carbamic acid, with which it is considered by some to be identical.

On exposure to the air bacteria develop in the urine, and, acting as a ferment, change the urea into ammonium carbonate, two molecules of water being at the same time taken up, thus :

$$CO(NH_2)_2+2H_2O=(NH_4)_2CO_3.$$

This gives rise to a change in the reaction of the urine, which after a time becomes increasingly alkaline, and the change is commonly spoken of as the alkaline fermentation of the urine. This change is extremely slow in solutions of pure urea, which do not support bacterial life.

With nitric and oxalic acids, urea forms sparingly soluble salts—a fact made use of in its preparation from urine.

The amount of urea eliminated in the 24 hours is about 500 grains (35 grammes). The amount varies (1) in some degree with the amount of urine secreted ; an increase in the amount of water being accompanied by a slight increase in the urea eliminated. Some materials, such as common salt, increase the water, and thereby also increase the urea. (2.) The character and quantity of the diet influences most remarkably the quantity of urea given off, the amount increasing in direct proportion to the quantity of proteid consumed. Fasting causes a rapid fall in the amount of urea ; even in the later days of starvation it continues to fall, but very slowly. (3.) The amount differs with age, being relatively greater in childhood than in the adult (about half as much again in proportion to the body weight). (4.) Many diseases have a marked influence on the amount of urea. In most febrile affections it increases with the intensity of the fever, while in disease of the liver it often notably decreases.

In diabetes, if the consumption of food be very great the daily excretion of urea may reach nearly 4 oz. (100 grammes) or three times as much as normal.

Preparation.—To obtain urea from human urine it is evaporated to one-sixth of its bulk, an excess of nitric acid is added, and it is left to stand in a cool place. Impure nitrate of urea separates from the fluid as a yellow crystallized precipitate. This insoluble salt is caught on a filter, dried, dissolved in boiling water, mixed with animal charcoal to remove the colouring matter, and filtered while hot; when the filtrate cools, colourless crystals of nitrate of urea are deposited. The precipitate is dissolved in boiling water, and barium carbonate added as long as effervescence takes place, barium nitrate and urea being produced. This is evaporated to dryness, and the urea extracted with absolute alcohol, which on evaporation leaves crystals of pure urea.

Estimation.—Urea can be estimated volumetrically by the method of Liebig, which depends on the power of mercuric nitrate to give a precipitate with it. The sulphates and phosphates must be first removed by the addition of 40 c.c. of a mixture of 1 volume saturated barium nitrate and 2 volumes saturated solution of caustic baryta, to an equal volume of urine. This is filtered, and from the filtrate an amount corresponding to 10 c.c. urine is taken. Into this known volume of urine a standard solution of mercuric nitrate (of which 1 c.c. corresponds to 1 centigramme of urea) is dropped until a sample drop of the fluid, mingled on a watch-glass with a drop of concentrated sodium carbonate solution gives a yellow colour, which indicates that some free mercuric nitrate remains. For every cubic centimetre of the standard mercuric solution used, there will be 1 centigramme of urea in the sample of urine; a small reduction has to be made for the chlorides, which are present in tolerably constant amount.

Another simple method consists in mixing together known quantities of urine and sodium hypobromite ($Na\,Br\,O$) with excess of caustic soda. The urea is decomposed in the presence of this salt, and free nitrogen evolved—

$$CON_2H_4+3(NaBrO)+2(NaOH)=3NaBr+Na_2CO_3+3H_2O+2N.$$

The quantity of urea may be determined by ascertaining the volume of nitrogen, which can be measured directly in a graduated tube.

Uric acid, of which the formula is $C_5H_4N_4O_3$ or $C_3H_2O_3(NH.CN)_2$, is present only in extremely small quantities in the normal urine of mammalia, but in birds, reptiles, and insects it forms the chief ingredient of the renal secretion. It is sparingly soluble in water, and insoluble in alcohol and ether. However, in solutions of the neutral phosphates and carbonates of the alkalies it combines with some of the base, so as to form acid salts, and at the same time converts the neutral into acid phosphates, to which, as has been already stated, the urine owes its acid reaction. These salts are more soluble in warm than in cold water, and hence generally fall as a sediment when the urine cools. Uric acid is readily converted into urea by oxidation, and is probably one of the steps in the formation of urea which commonly occurs in the body during the gradual oxidation of the proteid bodies.

The presence of uric acid may be recognised by the murexide test. The substance to be tested is gently heated in a flat capsule with some nitric acid. A decomposition occurs, N and CO_2 going off, urea and alloxan remaining as a layer of yellow fluid. If this be cautiously evaporated, and a drop of ammonia added, a striking purple-red colour is produced, which the addition of potash turns blue.

The amount of uric acid normally follows pretty closely the variations in urea, but is usually only about 8 grains (·5 gramme) per diem. In certain diseases the quantity may be much increased. For the quantitative estimation, which is seldom decided by the practitioner, the student must consult the text-books of physiological chemistry.

Kreatinin ($C_4H_7N_3O$) is always present in urine, probably being formed from kreatin by the loss of one molecule of water. About 15 grains (1 gramme) is excreted per diem.

Xanthin ($C_5H_4N_4O_2$) also occurs in urine, but in extremely small quantities.

Hippuric acid ($C_9H_9NO_2$) is a normal constituent of human urine, occurring, however, in very small quantities. On the other hand, it is one of the most important nitrogenous constituents of the urine of the herbivora, where it takes the place of uric acid. Its presence depends on the existence of certain ingredients (benzoic acid, &c.) in the food, which are capable of combining with glycin, and forming a conjugated acid, a molecule of water being formed at the same time, thus—

$$\begin{array}{ccccccc} \text{Benzoic Acid.} & & \text{Glycin.} & & \text{Hippuric Acid.} & & \text{Water.} \\ C_7H_6O_2 & + & C_2H_5NO_2 & = & C_9H_9NO_3 & + & H_2O. \end{array}$$

The amount of hippuric acid increases with increased consumption of vegetable food, in the cellulose of which the materials exist that are required for its formation. It is in the liver that the union between the glycin and the benzoic acid takes place, as is proved by the removal of that organ, when benzoic acid injected into the portal vein appears unchanged in the urine.

Oxalic acid ($C_2H_2O_4$) occurs often but not constantly in the urine. It is generally united with lime. It is said to appear in greater quantity, together with an excess of uric acid, after meals, and therefore to be related to the production of the latter in the body; but it probably is chiefly derived from oxalates being contained in some materials taken with the food.

COLOURING MATTERS.

It appears probable that the colour of the urine depends on the presence of small quantities of distinct substances which have different origins in the body. Three such have been described, and may be taken provisionally to represent our knowledge of the subject:—

1. *Urobilin*, which is an outcome of the colouring matter of the bile, and therefore a remote derivative of the colouring matter of the blood, is frequently present in the urine. It is probably the same as hydrobilirubin, some of which is occasionally absorbed from the intestinal tract and eliminated by the kidneys.

2. *Urochrom* is said to be the special pigment of the urine. It oxidises on exposure, forming a reddish substance that gives the dark colour to some urinary sediments (*Uroerythrin*).

3. A certain material (*Indican*) capable of producing *Indigo*, is commonly present in the urine of man, and in greater quantity in that of some animals, particularly the horse. It is supposed to be formed from the indol that arises from the putrefactive changes consequent on the pancreatic digestion. The indol is absorbed and unites with sulphuric acid to form Indican, which is a yellow substance. Under certain conditions it can be converted by oxidation into indigo-blue.

INORGANIC SALTS.

The urine is the great outlet for all inorganic salts. The most important of these are—

Common salt (NaCl.) of which a very variable, but always considerable amount passes away in the urine. The average quantity excreted per diem may be said to be about half an oz. (15 grammes). It depends greatly on the quantity taken with the food, and falls during starvation, but does not completely disappear. It is said that if absolutely no sodium chloride be taken with the food the quantity excreted diminishes greatly, and that albumin appears in the urine about the third day. The amount of salt eliminated follows, with striking accuracy, the changes that take place at different times and under different circumstances, in the quantity of urea excreted. These facts seem to indicate that there is some relationship between the secretion of the two bodies, or that sodium chloride participates in the chemical changes of the nitrogenous tissues. In many diseases there occur variations in the quantity of common salt in the urine, which can hardly be explained by the change in, or absence of food.

Phosphates.—About 60 grains (3 to 4 grammes) of phosphoric acid is excreted daily in the urine, being combined with alkalies to form salts, viz., potassium, sodium, calcium, and magnesium phosphates.

Sulphates.—Nearly 40 grains (2 to 3 grammes) of sulphuric acid, as sulphates of alkalies, are daily got rid of in the urine. The acid comes partly from the food, but chiefly from the oxidation of the sulphur contained in the proteids of the tissues.

A considerable quantity of *potassium*, *sodium*, *calcium*, and *magnesium*, combined as already mentioned, or with chlorine, is contained in the urine.

Small traces of *iron* are also always present in the urine.

Gases.—The urine also contains free CO_2, N, and some O. 100 volumes of gas pumped out of fresh urine have been found to consist of—

CO_2 = 65·40 per cent.
N = 31·86 „
O = 2·74 „

Abnormal Constituents.

Different kinds of substances occur in urine under circumstances of special physiological interest, and therefore may be here enumerated, although their accurate study belongs rather to pathology. First amongst these to be named is,—

Albumin, which occurs from (1) any great increase in the blood-pressure in the renal vessels, whether caused by increased inflow or impeded outflow. (2.) Excess of albumin in the blood, and, strange to say, some forms of albumin escape much more readily than others. Thus, egg albumin, globulin or peptone, if introduced artificially into the blood, are soon found in the urine. (3.) A watery condition of the blood, such as would give rise to œdema elsewhere. (4.) Total abstinence from NaCl. for some time. (5). Extensive destruction of the epithelium of the urinary tubes.

Next in importance to albumin are the following :—

Grape sugar; of which normally only the merest trace occurs in the urine although there is always a certain quantity in the blood. It is present in large quantities in (1) the disease known as diabetes, when a great quantity of pale urine with a very high specific gravity is passed. (2.) After injury of a certain part of the floor of the 4th ventricle of the brain. (3.) After poisoning by curara, carbonic oxide, and nitrate of amyl. In short any disturbance of the circulation of the liver gives rise to an increase of sugar in the blood, and when the amount reaches 6 per cent. it appears in the urine.

Bile Acids and *Pigments* appear in the urine when, from occlusion of the bile ducts, they find their way into the blood.

Leucin and *Tyrosin* also occur in the urine, but only after profound interference with the function of the liver.

The urine undergoes important changes after being voided, the explanation of which is of much interest to the practitioner, and must be understood by the student of medicine. (1.) Commonly enough the urine loses its transparency as soon as it gets cold, though perfectly clear when passed, or when again heated to the body-temperature, for the urates are soluble in warm but almost insoluble in cold water. This "muddiness," which soon settles down, as a more or less brightly coloured sediment, is chiefly caused by the precipitation of acid sodium urate, stained with a colouring matter derived from the urochrome. When this occurs the urine will always be found to be distinctly acid, and if it be left standing for some time in a cool place, the acidity will be found to increase, owing to the presence of a peculiar fungus which sets up *acid fermentation.* This is said to depend on the formation of lactic and acetic acids, and crystals of uric acid, amorphous sodium urate, and crystals of lime oxalate are deposited.

After a certain time (which is shorter when the urine is not very acid and is exposed to a warm atmosphere) the development of bacteria occurs in it, and causes the urea to unite with water, and to change in the manner already mentioned (p. 330) into ammonium carbonate. This gradually neutralises the acidity, and finally renders the urine alkaline. At the same time an amorphous precipitate of lime phosphate appears, and crystals of ammonio-magnesium phosphate and of ammonium urate are produced.

URINARY CALCULI.

Various ingredients of the urine, which are difficult of solution sometimes become massed together as concretions, particularly if there exist any small foreign body in the bladder, which, by acting as a nucleus lays the foundation of a stone. Sometimes small concretions are formed in the tubes or pelvic recesses of the kidney, and, when these make their way into the bladder, they commonly grow larger and larger. The structure and composition of a calculus often gives the history of its own transit from the kidney, and also of various changes in the metabolism of the individual, for successive layers of different substances are generally found in a stone that has attained any great size. The chief materials found in calculi are—uric acid, ammonium urate, calcium oxalate and carbonate, ammonio-magnesium phosphate, &c.

SOURCE OF UREA, &c.

The question as to whether the chief materials of the urine preexist in the blood and are therefore merely removed by the kidney, or are manufactured by the special powers of the renal cells, has been widely discussed, and though the great weight of evidence is in favour of the former view, some of the experimental results on the subject are rather conflicting.

The following are the more important points in the argument :—

1. The blood does normally contain most of the important substances found in the urine; so they need not necessarily be made in the kidney.

2. The blood in the vessel leading to the kidney—the renal artery—is said to contain more urea than the vessel leading from it —the renal vein—so that the blood appears to lose urea in passing through the kidney.

3. If the ureters be tied and the elimination be thus prevented, urea accumulates in the blood. This can hardly be made by the kidney, because—

4. If the renal arteries be tied so that no blood goes to the kidneys to effect the elaboration of urea in those organs, then the same accumulation results, showing that the kidneys are certainly not the only organs where urea is made.

5. Extirpation of the kidneys also gives rise to a great increase of the urea in the blood. The amount of urea in the blood after nephrotomy is said to increase steadily with the time which elapses after the operation, and the amount accumulated corresponds to the amount that would normally have been excreted in the same time, had the animal not been operated upon.

6, Lastly. In some diseases which greatly interfere with, or quite suppress the secretion of the kidneys, an accumulation in the blood of certain poisonous or injurious materials takes place, and gives rise to the gravest symptoms called uræmic poisoning, which closely coincide with those observed in experimental annihilation of the renal function.

From the foregoing it would appear to be satisfactorily settled *that* the urea, which is by far the most important ingredient of the secretion of the kidney, is probably made elsewhere and not in that organ, whose duty seems to be chiefly to remove it from the blood. This is most probably also true of all the other organic constituents of the urine. The question then arises :—Where is the urea formed ?

We naturally turn for an answer to the most wide-spread and most actively changing nitrogenous tissue, namely muscle. Here, however, we find no response, for neither does muscle contain much urea, nor does any very active muscular work perceptibly increase the general urea elimination. In muscle, however, a material closely allied to and readily convertible into urea, namely kreatin, occurs, and it has been suggested that this substance is changed into urea in the kidney. This cannot explain the origin of all the urea which appears in the urine, for, as already remarked, the urea excretion does not correspond with the muscle metabolism.

Without for one moment doubting that some, probably a considerable quantity of urea comes from muscle, which forms so large a part of our bodies, we conclude that there must be and assuredly are many other sources of urea, as there are many other parts or organs where nitrogenous textures are undergoing chemical changes and gradual waste.

One source of urea—the liver, is specially worthy of note, since it helps to explain the striking relation between the amount of albuminous food and the quantity of urea eliminated, the latter following immediately and running parallel with the former. There can be no doubt that most people consume much more albuminous food than is necessary for the adequate nutrition and preservation of the nitrogenous tissues, and therefore must have a surplus of nitrogenous material in their bodies. It may be remembered, as was pointed out in the chapter on digestion, that in all parts of the alimentary tract there is a limit to the absorption of peptones, and that in the small intestine when delay in absorption occurs the decomposition of peptones results, because in prolonged pancreatic digestion these peptones are changed into leucin ($C_6H_{13}NO_2$) and tyrosin ($C_9H_{11}NO_3$) and as such pass into the portal circulation to be borne to the liver. In the liver it is highly probable that these bodies are converted into urea, for, when they are introduced into the intestinal tract, they are absorbed and an excess of urea appears in the urine. Thus the excessive part of the proteid food, before it really enters the system, is broken up in the intestine into bodies which, notwithstanding the chemical difficulty of explaining the process, may be regarded as a step towards the formation of urea.

NERVOUS MECHANISM OF THE URINARY SECRETION.

With regard to the influence exerted by the nervous system on the renal secretion, we have but little satisfactory information, although there can be no doubt that here, as in other glands, the process is under the control of the nerves. Many of the circumstances which cause greater activity of secretion, such as taking large quantities of water, &c., have no effect on the general blood pressure, so that, if the increased flow be brought about by the vaso-motor mechanisms, it must be by means of nervous channels altering the blood flow in the special arteries of the glands. We know further that emotional conditions, such as hysteria, exist in which an unaccountably great quantity of urine of very low specific gravity is evacuated.

With regard to the effects of the vaso-motor nerves, we know that section of all the nervous twigs going to the kidneys causes great congestion and an immense increase in the secretion, which commonly contains albumin. This no doubt depends on the sudden rise in pressure in the glomeruli, owing to the dilatation of the arterioles. If the splanchnics, in which the renal vaso-motor nerves run, be cut, a great quantity of urine is produced from the same cause—vaso-motor paralysis—but, on account of the large area of vessels injured, the general blood pressure falls, and therefore the effect is not so much marked. If the peripheral end of the cut nerves be stimulated, the secretion is diminished, and, owing to spasm of the renal arterioles and fall of blood pressure in the glomerular capillaries, may be brought to a standstill. Section of the spinal cord at the 7th cervical vertebra stops the flow, because it so reduces the general blood pressure that the pressure in the renal vessels falls below that necessary for the filtration of the urine.

PASSAGE OF THE URINE TO THE BLADDER.

The pressure exerted by the blood in the glomerular capillaries is quite sufficient to make the urine flow from the pelvis of the kidneys into the bladder, because when the ureters are tied they become distended above the ligature by the urine flowing from the pelvis, where a pressure may be produced of some forty millimetres of Hg., at which pressure the secretion stops and becomes somewhat changed in chemical composition (kreatin appearing in greater quantity).

Normally, however, the passage of the urine along the ureters is accomplished by the peristaltic motion of the ducts, which goes on alternately in the two ureters, so that the urine flows into the bladder at different periods from the right and left kidney.

The ureters have a strong middle coat of smooth muscle along which a wave of contraction, lasting about one-third of a second, passes rhythmically in about 6 to 10 seconds from the pelvis of the kidney to the bladder.

Having reached the bladder, the urine cannot return into the ureters on account of the oblique way in which these ducts pass through the walls of the bladder. When the pressure in the bladder increases, the opening of the ducts becomes closed and acts as a kind of valve.

The urine, which is continuously secreted and rhythmically conveyed to the bladder, is only voided at convenient seasons; therefore special arrangements exist for its retention and expulsion.

The retention of urine in the bladder up to a certain point depends on the elasticity of the parts concerned, the dense elastic tissues around its outlet being able to resist the elastic force exerted by the viscera and the walls of the bladder upon its contents. Thus where no active muscular forces can possibly come into play, as in the case of the dead subject, or in complete paralysis following destruction of the spinal cord, a considerable amount of urine is retained. But when a certain pressure is attained by the gradual accumulation of urine within the bladder, the elasticity of the sphincter and the other tissues around the outlet is overcome by the elasticity of the bladder wall, and the urine slowly dribbles away.

In the normal condition there are two sets of muscular mechanisms which aid the elastic forces just named.

They may be regarded as antagonistic—the one, the sphincter muscle, by contracting, strengthens the elastic power of the tissues around the urethra which retains the urine; the other formed by the muscle-coat of the bladder, called the *detrusor urinæ*, as we shall see presently, is the chief agent in actively expelling the urine. When these muscles are in good working order, much more urine can be conveniently retained than the elasticity of the tissues about the urethra would permit of. If the spinal cord be destroyed the bladder can only retain about ⅓ the quantity of urine it conveniently holds when the cord is intact. We must, then, suppose that the sphincter muscle acts more powerfully when the elastic forces are equalized. The accumulation of urine after a certain time gives the sensation known as a full bladder, but this feeling is not necessarily accompanied by any immediate call to make water, though it soon produces a desire in that direction. We suppose, then, that the stimulus given to the sensory nerves by filling the bladder causes reflexly a constriction of the sphincter muscle, so that, in proportion as the pressure within the bladder increases, the resistance to its outflow is also augmented. This does not imply any automatic action of the sphincter vesicæ, but merely a constant reflex excitation of that muscle, which secures its contraction and the retention of a considerable amount of urine without the intervention of voluntary influences or attention.

Micturition, or the expulsion of the urine, does not normally ever depend on elastic forces alone, as in the case mentioned of paralytic incontinence, when the urine commences to dribble away as soon as a certain pressure is attained within the bladder.

When the bladder is full, the elastic forces tending to expel its contents increase, and, as we have seen, the resistance is proportionately augmented. Under ordinary circumstances, then, there is a combat going on between the expelling and retaining powers (neither the muscle in the wall of the bladder nor voluntary effort, however, coming into action), in which the retaining forces are just able to overcome the expelling elastic pressure. If the urine be retained for a considerable time, a moment arrives when the reflex stimulation of the sphincter no longer suffices to keep back the fluid, and the voluntary contraction of the neighbouring muscles has to be called to the aid of the sphincter. Under these circumstances, if a drop of urine make its way into the sensitive urethra matters are greatly altered. Now, even voluntary effort does not suffice to keep back the stream, and an imperative call is made upon the local mechanisms to empty the bladder. This is accomplished by the contraction of the muscular coat of the bladder, which is excited reflexly by the stimulus starting from the mucous membrane lining the urethra. The evacuation of the bladder is then accomplished quite independently of the will by a reflex act, which may even be unconscious.

When the urine once commences to flow it continues until the bladder is quite empty, the last drops of urine being expelled from the urethra by rhythmical spasms of the muscles around the bulbous portion of that canal. The sequence of events will then be—stimulation of the mucous membrane of the urethra by escape of urine, contraction of the detrusor urinæ; relaxation of the sphincter; rhythmical contraction of the ejaculator urinæ and finally a voluntary twitch of the levator ani and neighbouring muscles.

This sequence of events may go on in sleep, as a result of slight *local excitations*, frequently in children, when probably the sphincter is more readily fatigued.

Under ordinarily favourable circumstances, however, we micturate voluntarily, and the bladder is never allowed to become so over-distended that the reflex contraction of the sphincter is insufficient to retain the urine. Almost at any time we can call forth the reflex act just described by increasing the pressure on the bladder by voluntary contraction of the abdominal muscles; the diaphragm being depressed and fixed, the muscles of expiration are put into action, and the contraction of the sphincter muscle being at the same time probably checked by the will, the power of retention is overcome.

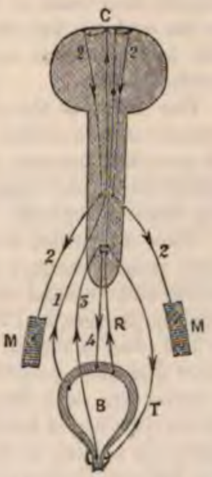


Fig. 176.—Diagram of the Nervous Mechanism of Micturition.

B. Bladder.
M. Abdominal muscles.
C. Cerebral centres.
R. Represents impulses which pass from the bladder to the centre in the spinal cord, whence tonic impulses are reflected and pass along T to sphincter, which retains the urine.

When the bladder is distended, impulses pass to the brain by 1, and when we *will*, the tonus of the spinal centre stimulating the sphincter is checked, and the abdominal muscles are made by 2 to force some urine into neck of bladder, whence impulses pass by 3 to inhibit the sphincter centre and excite the detrusor though 4.

The moment the balance of power is thus turned in favour of the expelling agencies and a drop of urine reaches the urethra, the excitation thus produced brings about the complete evacuation of the bladder without further voluntary effort.

The nervous mechanism that controls the act of micturition consists essentially of ganglionic centres which are situated in the lumbar enlargement of the spinal cord, and of two sets of nerve channels passing to and from this centre. The centres may be said to be composed of functionally distinct parts—a *retaining* and *evacuating* part. The retaining centre causes the sphincter muscle to contract. The evacuating centre can excite the detrusor to action while the sphincter is relaxed by the inhibition of its exciting centre. One set of nerve channels communicates between these centres and the urinary organs, and the other between the cord centres and the cerebral hemispheres. That which connects the special lumbar centres with the bladder, contains motor (efferent) fibres of two kinds, going to the antagonistic muscles, the sphincter vesicæ, and the detrusor urinæ respectively, and sensory (afferent) fibres of different kinds; those going from the bladder to the nerve cells in the cord which stimulate them and cause the sphincter to remain tonically contracted, and passing from the mucous membrane of the urinary passages to these ganglionic cells in the cord are two sets; one of which excites the contractions of the detrusor urinæ and the other inhibits the tonic action of the retaining centre.

The action of the ganglionic cells that stimulate the sphincter muscle can to a certain extent be either aided or checked by means of cerebral influences, so that two kinds of fibres—a stimulating and an inhibitory one—must pass from the hemispheres to the micturating centre in the cord.

Those cells which govern the motions of the detrusor seem to be least under voluntary control, and are probably only stimulated to action under normal circumstances by the impulses arising from the urinary passages, and hence are simply reflex centres.

The effect of certain emotions on the act of micturition seems to show that those ganglion cells in the cord which cause the bladder to contract are connected with the higher centres. Thus, extreme terror (in a dog at least) often causes a forcible expulsion of urine, and great anxiety or impatience seems in man often to have a checking influence, causing great delay in initiating micturition.

CHAPTER XXIII.

NUTRITION.

We can now compare the incomings and outgoings of the economy, and should now be in a position to see what light can be thrown by this comparison upon the actual changes which take place in the textures of the body.

We have seen that the income is made up of substances belonging to the same groups of materials as are found in the body, viz., albumins, fats, carbo-hydrates, salts, and water, introduced by the alimentary canal, and oxygen, which is admitted by the respiratory apparatus; whilst the outgoings consist of urea from the kidneys, carbonic acid from the lungs, certain excrement from the intestine and other mucous passages, sweat, sebaceous secretion, epidermal scales, from the skin; together with a quantity of water from all these ways of exit. The milk, ova, and semen, may be here omitted, being regarded as exceptional losses.

In order that the body may be kept in its normal condition, it is necessary, that the income should at least be equal to the outgoings of all kinds, and, except where growth is going on rapidly, an income equal to the expenditure ought not only to suffice, but be the most satisfactory amount of supply for the economy.

We know that animals can live for some considerable time without food, in which case, though there be no income, a certain expenditure is necessary to sustain life, and therefore the outgoings continue. We ought thus to be able to arrive in a very simple manner at the minimal expenditure necessary for the sustentation of the body. We shall find, however, that (1) an income equal to this minimal expenditure (starvation) does not at all suffice to keep up the body-weight, and that (2) a considerable margin over and above this minimum is necessary in order to establish the nutritive equilibrium; (3) further, that the proportion of material eliminated and stored up in the body respectively varies as the income is increased; (4) and finally, that the quality of the food—*i.e.*, the proportion of each group of *food-stuff* present in the diet—has an important influence on the quantity required to establish the equilibrium, or that best suited to cause increase of weight or to fatten.

It will be convenient to consider the following different cases in succession :

1. No income, except oxygen, *i.e.*, starvation.
2. An income only equal to the expenditure found during starvation.
3. Perfect establishment of nutritive equilibrium.
4. Excessive consumption.

TISSUE CHANGES.

As is well known, a deprivation of oxygen—by the respiratory function being stopped—almost immediately puts an end to the tissue changes necessary for life, so that the oxygen-income cannot be interfered with without instant death ensuing. Moreover, it has been found that a small supply of water makes the investigation of the various tissue changes more reliable, by facilitating them and prolonging life. We, therefore, commonly speak of a total abstinence from solids as starvation.

When deprived of food, those tissues upon whose activity life depends must feed upon the materials stored up in some part of the system. The first questions to discuss are how much the body loses daily in weight during the time that it is thus feeding on itself, and how far the different individual tissues contribute to this loss.

The general loss of weight is directly estimated by weighing the animal, and the loss of the individual tissues is calculated by a careful analysis of the various excreta, by which the exact amount of nitrogen, carbonic acid, &c., are ascertained : the nitrogen corresponds to the loss of muscle ; and the carbon (after excluding that portion which is the outcome of muscle change, which may be calculated from the nitrogen) corresponds to the fats oxidised.

It has been found that a starving animal loses weight at first rapidly, and subsequently more slowly ; and the reason for this difference is that during the first three or four days the benefit of the food last eaten continues, and the waste materials are eliminated in proportionately large quantity. When the influence of the food taken prior to the commencement of starvation has ceased, the daily amount of materials eliminated remains nearly constant, and the *body-weight* diminishes slowly until the animal's death.

Adult animals commonly live until they have lost about half of their normal body-weight. Young animals die when they have lost about 20 per cent. of their weight.

Roughly speaking, we may take the body of a man to be made up of the following proportions of the more important textures :—

Muscles	50 per cent.
Skin and fat	25 ,,
Viscera	12 ,,
Skeleton	13 ,,

Seeing that the muscle tissue contributes such a large proportion to the body-weight, we cannot be surprised that in starvation the greatest absolute loss occurs in this tissue ; except in the case of excessively fat animals. Next comes adipose tissue, which almost entirely disappears, the absolute loss from it varying in proportion to the fatness of the animal at the beginning of the investigation. The spleen and liver lose more than half their weight, and the amount of blood is greatly reduced. The smallness of the loss that occurs in the great nervous centres is very striking. They seem to feed on the other tissues.

The following table gives the approximate *per centage* of loss which takes place in each individual tissue during starvation :—

Fat	97·0 per cent.
Muscle	30·2 ,,
Liver	56·6 ,,
Spleen	63·1 ,,
Blood	17·6 ,,
Nerve centres	0· ,,

With regard to the portals by which the various materials make their escape, it has been found that practically all the nitrogen passes off with the urine, and about nine-tenths of the carbon escapes by the lungs as CO_2, the remaining one-tenth passing off by the intestine and kidneys. Three-fourths of the water is found in the urine, and one-fourth goes off from the skin and lungs.

The following table shows the items of the general loss, and the amount per cent. which passes out by the chief channels of exit :—

	Total Elimination.	Viâ Kidneys.	Lungs and Skin.	Excrement.
Water	995·34 grm.	70·2 per cent.	26·1 per cent.	3·7 per cent.
Carbon	205·96 ,,	6·4 ,,	92·6 ,,	1·9 ,,
Nitrogen	30·81 ,,	100·0 ,,	—	—
Salts	10·03 ,,	97 ,,	—	2·4 ,,

As the loss of weight of an animal's body during starvation is at first rapid and then more gradual, so also the amount of material eliminated is found to diminish much more slowly after the first few days. This is well seen from the nitrogenous elimination. For the first four days the fall in the amount of urea excreted is very rapid, it then decreases almost constantly until the death of the animal, only slightly decreasing in proportion as the animal slowly decreases in weight. This has led to the conclusion that the amount of nitrogenous material eliminated during ordinary circumstances with a full diet comes partly from used-up nitrogenous tissues, and partly from nitrogenous materials which have never really entered into the composition of the tissues, but rather are present as surplus or floating nitrogenous pabulum. Hence, two kinds of proteid are supposed to exist in the body, viz., (1) that forming part of the tissues, and (2) that circulating as a ready supply for the nutritive demands of the tissues.

In the second case mentioned, namely, where an amount of food is supplied which is just equal to the expenditure which was found to take place during starvation, one might suppose that the diet, though minimal, would yet suffice to preserve the normal body-weight. However, practice shows this to be far from what actually occurs.

An animal fed on diet equal in quantity to the outgoings during starvation continues to lose weight, and the quantity of nitrogenous substance eliminated (urea) is greatly in excess of the low standard found during complete abstinence from food. From this it would appear that even when supplied with an amount of nitrogenous material equal to that drawn from the tissues during starvation, an animal still takes a further supply from its own textures. Thus the body subsists on the scanty allowance of nutriment it borrows from the tissues during starvation, only so long as there is absolutely no food income, and the moment any food is supplied an increased expenditure is set up, the income is exceeded, and a deficit occurs which is best seen in the nitrogen balance.

It follows, then, that feeding an animal on an amount of food-stuffs exactly corresponding to the quantity of nutriment abstracted from its own textures during total abstinence is only a slower form of starvation.

With regard to nitrogenous substances, it has been proved that nearly three times as much as the amount eliminated during starvation is required to establish an equilibrium between the income and expenditure of those special substances, and that any less than this leads to a distinct nitrogenous deficit.

The third case mentioned in a previous paragraph (viz., in which the nutritive equilibrium is exactly maintained, so that the body-weight remains unaltered, the gain and loss being equal) is the most important one for us to determine, since its final settlement would enable us to fix the most beneficial standard of diet. Unfortunately, this case is also the most difficult upon which to come to a satisfactory conclusion, for the following reasons :

1. The elaborate nature of the conditions imposed during the experiment makes it difficult to carry on the investigation with scientific accuracy.

2. Even when the amounts of gain and loss exactly correspond we cannot say that we have the best dietary ; because some of the income may be quite useless, and pass through the economy without having any function to perform in it, and yet appear in the output so as to give an accurate balance.

3. We have just seen that the relative amounts of outgoings and of material laid by as store are altered and regulated by the quantity of income. And we find that the quality of the income, *i.e.*, the relative proportions of the various food-stuffs, has a material influence on the quantities of material laid by and eliminated respectively. We must, therefore, consider the efficacy of each of the groups of the food-stuffs when employed alone and mixed in different proportions.

4. Different animals seem to have different powers of assimilation ; and under various circumstances the requirements and assimilative power of the same animal may vary.

An animal fed upon a purely meat diet requires a great amount of it to sustain its body-weight. It has been found that from $\frac{1}{20}$ to $\frac{1}{25}$ of the body-weight in lean meat daily is necessary to keep an animal alive without either losing or gaining weight. If more than this amount be supplied the animal increases in weight, and as its weight increases a greater amount of meat is required to keep it up to the new standard. So that to produce a progressive increase of weight with a purely meat diet, it is necessary to keep on increasing the quantity of meat given. The reason of this is found in the fact that albuminous diet causes an increase in the changes occurring in the nitrogenous tissues.

If an animal which is in extremely poor condition be given an *ad libitum* supply of lean meat, only a limited portion of the albuminous substance is retained in the tissues. By far the larger proportion of the nitrogenous food is found given off and is represented in the urine by urea, and a comparatively small proportion is stored up. If this large supply of meat diet be continued for some time, less and less of the *albuminous material* is stored, more and more being eliminated as urea, until finally the urea excreted just corresponds to the albuminous materials in the ingesta. When only meat is given, it must be supplied in large quantities to maintain the balance of nitrogenous income and expenditure which is spoken of as nitrogenous equilibrium. Upon the occurrence of a change in the amount of nitrogenous ingesta, this nitrogenous equilibrium varies, and it takes some time to become re-established, because a decrease in the meat diet is accompanied by a decrease in the weight of the animal, and an increase causes it to put on flesh. For each new body-weight there is a new nitrogenous equilibrium, which is only attained after the disturbed relation between the nitrogenous ingesta and excreta has been re-adjusted.

The increase of weight which follows a liberal meat diet depends in a great measure on fat being stored up in the body. Much more of this material is made than could come from the fat taken with the meat; hence, we must conclude that it is made from the albuminous parts of the meat.

The effect of a diet without any albuminous food is that the animal dies of starvation nearly as soon as if deprived of all forms of food, with the exception that the weight of the body is much less reduced at the time of death.

The addition of fats and sugars to meat diet allows a considerable reduction to be made in the supply of meat, and both the body-weight and nitrogenous tissue change can be kept in equilibrium on a smaller amount of food. It has been estimated that the nitrogenous tissue change is reduced 7 per cent. by the addition of fat, and 10 per cent. by the addition of carbohydrate food to the meat diet; therefore less meat is wanted to make up nitrogenous tissues. Further, fats and sugars, which obviously cannot of themselves form an adequate diet, since they contain no nitrogen, seem to have the power of accomplishing some end in the economy which, in their absence, requires a considerable expenditure of nitrogenous materials to bring about. Fats and sugars, then, supply to the body readily oxidisable materials, and thus shield the albuminous tissues from oxidation, as well as reduce absolutely the nitrogenous metabolism.

It would further appear from the experience gained from the stall-feeding of animals that a good supply of carbohydrates, together with a limited quantity of nitrogenous food, is admirably adapted to produce fat. Since much more fat has been found to be produced in pigs than could be accounted for by the albuminous and fatty constituents of their diet, we must suppose that from their carbohydrate food fat can be manufactured in their body.

Much of the difficulty found in reconciling the opinions of different authors upon this point can be removed, and a general idea of the manufacture of fats from various food-stuffs can be gained, by bearing in mind the assimilative and secretive functions of the protoplasm. There can be no doubt whatever that the active protoplasm of many parts and organs if properly nourished can manufacture fat. As examples, we may take the liver and mammary cells, and those connective tissue cells which have no great nutritive duty to attend to. This fat production by the protoplasm may be regarded as a secretion of fat, though only in one of the examples given does it appear externally as a definite secretion—milk. We cannot scrutinise the chemical methods by which this change is brought about in protoplasm, any more than those which give rise to any other secretion. We know that protoplasm uses as pabulum, albumin, fat, and carbohydrate, and we have no reason to doubt that the proportion of these materials found to form the most nutritious diet for the body generally, is also the proportion in which protoplasm can best make use of them. Probably such cells as part with a material containing nitrogen—such as mucin-yielding gland cells—require a greater proportion of pabulum containing nitrogen (albumin) for their perfect function. Probably those cells which produce a large quantity of non-nitrogenous material do not require more nitrogen than is necessary for their perfect re-integration as nitrogenous bodies. But for their active function, *i.e.*, the manufacture of their secretion, they only require a pabulum which contains the same chemical elements as are to be found in the output. In the case of fat-formation, then, a supply of fat or carbohydrate ought to suffice if accompanied by a small amount of albuminous substance. If these non-nitrogenous substances be withheld, the protoplasm can no doubt obtain the quantity of carbon, hydrogen, and oxygen requisite to manufacture fat from albumin, and thus a large amount of nitrogen will be wasted.

There is nothing in the foregoing statement that is not in accord with the results of practice and experiment.

Fat cannot be produced without nitrogen in the diet, because the fat-manufacturing protoplasm cannot live without nitrogen, which is absolutely necessary for its own assimilative re-integration. A good supply of nitrogenous food aids in fattening, since it gives vigour to all the protoplasmic metabolisms, and among them fat-formation.

The albuminoid substance *gelatine*, which is an important item in the food we ordinarily make use of, is able to effect a saving in the albuminous food-stuffs. Although it contains a sufficiently large *proportion of nitrogen*, it cannot satisfactorily replace albumin in the food. Indeed, in spite of the great similarity in its chemical composition to albuminous bodies, it is hardly a better substitute for proteids than fat or carbo-hydrate ; and, although an animal uses up less of its tissue nitrogen on a diet of gelatine and fat than when it is fed on fat alone, it soon dies, as if its diet contained no nitrogenous substance.

The last case we have to consider is that in which the supply of food-material is in excess of the requirements of the economy. This is certainly the commonest case in man.

Much of the surplus food never really enters the system but is conveyed away with the fæces.

In speaking of pancreatic digestion, reference has been made to the possible destiny of excess of nitrogenous food. In the intestine, some of it is decomposed into leucin and tyrosin, which are absorbed into the intestinal blood-vessels. In the body these substances undergo further changes, which probably take place in the liver. As a result of the absorption of leucin, a larger quantity of urea appears in the urine, and hence the leucin formed in the intestine by prolonged pancreatic digestion, is a source of urea. (See pp. 125, 337.) This view is supported by the almost immediate increase in the quantity of urea eliminated when albuminous food is taken in large quantity.

From the fact that a considerable amount of fat may be stored up by an animal supplied with a liberal diet of lean meat, we must conclude that part at least of the surplus albumin goes to form fat. It has been suggested that after sufficient albumin has been absorbed for the nutritive requirements of the nitrogenous tissues, the rest is split up into two parts, one of which is immediately prepared for elimination as urea by the liver, and the other undergoes changes, probably in the same organ, which result in its being converted into fat.

It would further seem probable, from the manner in which the urea excretion changes during starvation, that, as before mentioned, the absorbed albumin exists in the economy in two forms: one in which it has been actually assimilated by the nitrogenous tissues and forms part of them, and hence is called organ-albumin ; the other, which is merely in solution in the fluids of the body, being in stock, but not yet absolutely assimilated, and hence called circulating albumin. The latter passes away during the first few days of starvation, being probably broken up to form urea, and a material which serves the turn of non-nitrogenous food. The organ-albumin only appears to be used for the formation of urea after the circulating albumin has completely disappeared.

From the foregoing it will be gathered that we cannot say what are the exact destinies of the various food-stuffs in the body. Proteids are not exclusively utilised in the re-integration of proteid tissues, as an excess gives rise to a deposit of fat. Carbohydrates are not turned into glycogen in the tissues simply to replace the carbohydrates used, but as will be shown when speaking of muscle metabolism, they are intimately related to the chemical changes which take place during the activity of that tissue. If fats are chiefly devoted to the restitution of the fat of the body, they certainly are not the only kind of food from which fat can be made.

We may say, then, that all food-stuffs are destined to feed the living protoplasm, whether it be in the form of gland cells, the cells of the connective tissues, or muscle-plasma, so that all the food-stuffs that are really assimilated contribute to the maintenance of protoplasm and subserve to its various functions. Besides nourishing itself and keeping itself up to a certain standard composition, protoplasm, or rather the various protoplasmata, can make the various chemical materials we find in the body. Some produce fat, some animal starch (glycogen), and others manufacture the various substances we find in the secretions; while yet another group is devoted to setting free and utilising the energy of the various chemical associations.

But all the food we eat is not assimilated; indeed, the destiny of the numerous ingredients of our complex dietaries is not easily traced. Of food-stuffs proper the following classification may be made, showing that even the same stuff may meet with a different fate under different circumstances—

1. Stuffs which never enter the economy (fæces).
2. Materials absorbed and arriving at the blood are at once carried to certain portals of excretion (excess of salts).
3. Substances which are broken up in the intestine to facilitate their elimination (excess of proteid).
4. Substances absorbed and carried along by the fluids, but not really united to the tissues (circulating albumin).
5. Materials which after their absorption are really assimilated by the protoplasm of the tissues (a certain amount of all food-stuffs).
6. Substances which, after their assimilation by the protoplasm, re-appear in their original form, and are stored up (fats).

The question of the exact amounts and materials required to form *the most economic and* wholesome dietary is one of too great practical importance to receive adequate attention in this manual. As a rule men, like other animals, partake of food largely in excess of their physiological requirements when they can get it. This may be seen by contrasting one's own daily food with the amount which has been found to be adequate in the case of individuals who have not the opportunity of regulating their own supplies of comestibles.

An adult man should be well nourished if he be supplied with the following daily diet:—

Albuminous foods .	100 grms.	or	3·5 ozs.
Fats	90 „	„	3·1 „
Starch	300 „	„	10·7 „
Salts	30 „	„	1·0 „
Water.	2800 „	„	5 pints

As a matter of fact, many persons do thrive on a much less quantity of proteid than that given in this table, but in their case the fats and starches should be proportionately increased.

Such a dietary could be obtained from many comestibles alone, and hence the taste of the individual may be exercised in selecting his food without much departing from such a standard. Individual taste commonly selects foods with too much proteid—*i.e.*, an excess of nitrogen—whilst the cheapness of vegetable products dictates their use in greater abundance as food.

Compare Chap. V., p. 68, where the quantity of the different food-stuffs in some of our common articles of diet is given.

CHAPTER XXIV.

ANIMAL HEAT.

PART of the work done or energy set free by the chemical changes in the animal tissues appears as heat which is devoted to keeping the body warm ; for the bodies of most animals are considerably warmer than their surroundings. Warm-blooded animals are those which habitually preserve an even temperature independent of the changes which take place in that of the medium in which they live ; and, as the term warm-blooded implies, their temperature is as a rule higher than the surrounding air or water. Cold-blooded animals on the other hand are those whose temperature is considerably affected by, or more or less closely follows, that of the medium surrounding them.

The blood of all mammalia has pretty much the same temperature as that of man, about 37·5° C., and probably varies under similar circumstances. But birds, the other class of warm-blooded animals, have a temperature about 4° or 6° C. higher than that of mammals.

The blood of those animals whose temperature follows the changes that occur around them, is generally from 1° to 5° C. higher than the medium in which they live. They produce some heat, though it be in small quantity, and since they have no special plan for its regulation, it does not remain at a certain standard. Wherever active oxidization takes place, heat is produced ; so even in invertebrate animals an elevation of temperature occurs ; this can be easily ascertained when they exist in masses, as bees, an active hive sometimes reaching a temperature of 35° C.

Instead of the term "warm-blooded," it is more accurate to apply to animals whose temperature remains uniformly even, and independent of their surroundings, the term "*Homœothermic*" (constant-temperature), and to animals with temperatures varying with their surroundings "*Poikilothermic*" (or changing temperature), instead of the words warm- and cold-blooded.

MEASUREMENT OF TEMPERATURE.

On account of the slight degrees of variation that occur in the temperature of man, all the changes taking place can be measured with a thermometer having a short scale of some 20 degrees, each degree of which occupies considerable length on the instrument, so that very slight variations may be easily appreciated. Such thermometers, with an arrangement for self-registering the maximum height attained by the column of mercury, are in daily use for clinical observation, for the temperature of the body is now a most important aid to diagnosis and prognosis in a large class of diseases.

As heat is constantly being lost at the surface of the body, the skin is colder than the deeper parts, and in order to avoid variations caused by this surface loss—which depends in a measure on the temperature of the air—special arrangements are necessary to prevent the thermometer being too much influenced by it. The instrument may be brought into close proximity to the deeper parts by being introduced into one of the mucous passages, where it is surrounded by vascular tissue. In animals the rectum is the most convenient part for the application of the thermometer, but in clinical practice it is usually placed under the tongue, or in the arm-pit, the bulb being held so that on all sides it is in contact with the skin and protected from the cool air.

The variations at different parts of the body are but slight, and the average normal temperature in man is found to be about 37° C.

NORMAL VARIATIONS IN TEMPERATURE.

The normal temperature undergoes certain variations, some of which are—(1.) Regular and periodical, depending upon the time of day, the ingestion of food, and the age of the individual. (2.) Accidental circumstances, such as mental or bodily exertion.

a. The temperature is highest between 4 and 5 P.M. and lowest between 2 and 4 A.M., the transition being gradual. This diurnal variation, which normally does not much exceed 1° C., is much exaggerated in hectic fever.

b. The temperature rises after a hearty meal and falls during fasting. During starvation the temperature sinks gradually until the death of the individual.

c. The temperature is highest at birth, and falls about 1° C.

between that and the age of 50 years,—in extreme old age it is said that it again rises.

d. Muscular exertion, which gives the individual the sensation of great warmth, only changes the temperature of the blood about ·5° C. The very high temperature which accompanies the disease Tetanus, where all the muscles are thrown into a state of spasm, probably depends more on pathological changes than on muscular action.

e. Mental exertion is also said to cause a rise of temperature.

f. Slight differences in the heat of the blood may be brought about by variations in the surrounding temperature. The abnormally high temperature of fever is much more easily affected by changes in the rate of removal of the heat from the body, than is the normal temperature, and hence the therapeutic value of cold applications in this class of diseases.

The temperature of different parts of the body varies in a slight degree, and depends upon the following circumstances:—1. The amount of blood flowing through them; for the blood is the great carrier of warmth from one part to another, supplying heat where it is lost by exposure, &c., and it conveys material to those parts where the heat is generated. 2. The amount of heat produced in a given part, *i.e.*, the activity of its tissue change. 3. The amount of heat lost, which depends on (*a*) the extent of surface; (*b*) the external temperature; (*c*) the power of conduction of, and the capacity for heat of the surrounding medium.

From this it is obvious that the deeper parts of the body, where active chemical change takes place and which are protected from exposure, must be warmer than the exterior, which is constantly losing its heat to the air. The blood then which flows through the surface vessels is cooled, and that which flows through the deeper vascular viscera is warmed. Thus the skin is usually about 37° C., while the mouth beneath the tongue is about 37·5° C., and the rectum about 38° C. Accordingly, then, as the blood has recently passed through a part of the body where it has had an opportunity of losing or gaining heat, its temperature varies, but only within narrow limits. The mean temperature of the blood is higher than that of any other tissue. The blood in the hepatic capillaries is the warmest in the body. This reaches 40·73° in the dog, or nearly two degrees higher than that in the aorta of that animal. The cool blood from the extremities and head mingling in the right side of the heart with the unusually warm blood from the liver keeps the blood going to the lungs at the standard temperature. The blood in the left side of the heart is a little cooler than the right, probably because the latter lies on the warm liver, as is proved by the substitution of a cold object for this organ, when the temperature is reversed, and the blood on the right side becomes colder than the left. It is not because the blood is cooled going through the lungs, for the heat used in warming the respired air is given off by the nose and other air passages and not by the alveoli of the lungs.

Mode of Production of Animal Heat.

It has already been indicated that the general effect of the tissue change of the body is a kind of combustion in the tissues of certain substances obtained from the vegetable kingdom, viz. proteid, fat, carbo-hydrate, &c. The combustible substances are capable of being burned in the open air, or made to unite with oxygen so as to produce a certain amount of heat, being thus converted into CO_2 and H_2O. In the body the oxidation goes on in a gradual or modified way, and the end products of the process can be recognised as CO_2 eliminated from the lungs, and as water and urea got rid of by the kidneys. The general tendency of the chemical changes in the tissues is such as will set free energy in the form of heat.

The amount of heat that any substance is capable of giving off corresponds to the amount of energy required for the formation from CO_2 and H_2O, &c., of the compounds contained in it, and this correspondence remains whether the dissociation take place rapidly or slowly. The substances we make use of as food have thus a certain heat value which depends upon their chemical composition.

The high temperature which homœothermic animals can keep up in spite of the cold of the atmosphere in which they live is readily accounted for by the chemical change which is constantly occurring in the tissue of their bodies.

The amount of heat produced in any part must, then, depend upon the activity of its tissue change, for we find that the temperature varies with the elimination of CO_2 and urea, which give a fair estimate of the chemical changes of the tissues.

1. The diurnal changes in temperature are accompanied by an afternoon increase and a morning decrease of CO_2 and urea.

2. The tissue change giving rise to CO_2 decreases in a fasting animal, as does also the production of heat.

3. *More* CO_2 is eliminated after meals, when the temperature also *rises.*

4. The activity of various organs, such as the muscles and glands, is associated with a local increase of temperature.

Income and Expenditure of Heat.

As repeatedly stated, the chemical changes which give rise to the heat, cause a certain waste of the tissues, which have again to be renewed by the assimilation of various nutrient materials. The food is thus really the fuel of the animal body, and the peculiarity of this form of combustion is that the tissues assimilate or convert into their own substance the fuel, and then themselves undergo a kind of partial combustion by means of which they perform their several functions, amongst others heat-production.

As already mentioned, heat is produced most abundantly in those tissues which undergo most active chemical changes, hence the protoplasmic cells of glands and the contractile substance of muscle must be looked upon as the chief agents in setting heat free.

The possible heat-income depends on the amount of nutrient matter assimilated. As each kind of food has a certain heat value, *i.e.*, the number of heat-units its combustion will produce, we ought to be able to estimate the amount of heat produced by ascertaining this value and subtracting the calorific value of the various substances given off by the body. Since practically the temperature of the body remains the same, the amount of heat lost during a given time should correspond to the income estimated from the number of heat-units of the food. So far, however, attempts to make the calculated heat-income correspond with the expenditure have not been productive of satisfactory results, the estimated calorific value of the food being hardly equal to the heat calculated to be given off by the body. We must remember that it is not the proteid, fat and starch of the food that we burn, but the living tissues formed by the assimilation of these substances. We do not know what chemical changes go on in the steps of tissue formation, and therefore we cannot say exactly what combinations are submitted to the combustion which gives us a high heat-value.

Since the activity of muscle and gland tissue is constantly undergoing variations in intensity, the amount of chemical change differs at different times, so that the amount of heat produced must also vary. We know that the heat set free by any organ, such as a gland or a muscle, increases in proportion to the increase of its functional activity, but we cannot say that the calorific activity can vary *independently of other* circumstances. Without such a special calorific function of some tissues, such as muscle, the actual net heat-income must vary with circumstances which are accidental and therefore irregular.

Since we know that the nervous system controls the tissue activities which are accompanied by the setting free of heat, we can see how the nerve centres can materially influence the heat production of the body; thus the more active are the muscles, glands, &c., which are under the control of nerves, the greater the amount of heat produced in a given time. That the nervous system can cause in any tissue a chemical change, giving rise to a greater production of heat, without any other display of functional activity, we do not know, but many facts seem to point to such a possibility.

The effect of nerve influence on the production of heat is greatly complicated also by the enormous power exercised by the nerves over the blood supply through the means of the vaso-motor mechanisms, for the temperature of any given part is so intimately related to the amount of blood flowing through it that the former has been commonly accepted as an adequate measure of the latter.

For the present, therefore, we are not in a position to speak with decision of nerves with a purely thermic action.

The expenditure of the heat may be classed under the following headings:

1. In warming ingesta: As a rule all the food and drink we make use of as well as the oxygen we breathe are colder than the body, and before they pass out they are raised to the body temperature.

2. Radiation and Conduction: From the surface of the body a quantity of heat is being expended in warming the surrounding medium, which is habitually colder than our bodies. The colder the medium, the greater its capacity for heat, and the more quickly it comes in contact with new portions of the surface the more warmth it robs us of. Water or damp air takes up much more heat from our surface than dry air of the same temperature, and the quantity of heat lost is still further increased if the medium be in motion, so that the relatively colder fluid is constantly renewed.

3. Evaporation: (a.) From the air passages; a quantity of water passes into the vaporous state and saturates the tidal air, and this change of condition from liquid to that of vapour absorbs much heat; (b.) From the skin: surface evaporation is always going on, even *when no moisture* is perceptible on the skin, and much fluid of which *we are not* sensible is lost in this way. The quantity of heat lost by

evaporation from the skin will depend on the temperature and the degree of moisture of the air in proportion to that of the surface of the body.

As has been said, the exact income of heat is uncertain and variable because the data upon which the absolute amount can be calculated are not scientifically free from error. According to the most careful estimates an adult weighing 82 kilo. produces 2,700,000 units of heat in the twenty-four hours which are expended in the following way :—

In warming ingesta	70,157	units of heat.
warming tidal air	140,064	" "
By the evaporation of 656 grm. water from the air passages	397,536	" "
By surface loss	2,092,243	" "

From this it appears that more than three-quarters of our heat is lost by the skin (77·5 per cent.) ; by pulmonary evaporation, 14·7 per cent. ; in heating the air breathed, 5·2 per cent. ; in heating ingesta, 2·6 per cent.

MAINTENANCE OF UNIFORM TEMPERATURE.

In order that the vital processes of man and the other homœothermic animals should go on in a normal manner, it is necessary that their mean temperature remain nearly the same, and we have seen that under ordinary circumstances it varies only about one degree below or above the standard 37° C., notwithstanding the changes taking place in the temperature around us. Thus we can live in any climate, however cold or warm, and so long as our body temperature remains unaltered, we suffer no immediate injury.

There is a limit however to this power of maintaining a uniform standard temperature. If a mammal be kept for some time in a moist medium, where evaporation cannot take place, at a temperature but little higher than its body, say over 45° C., its temperature soon begins to rise and it dies with the signs of dyspnœa and convulsions (probably from the nervous centres being affected) when its temperature arrives at 43°—45°. If placed in water at freezing point an animal loses its heat quickly, and when its body temperature has fallen to about 20° C. it dies in a condition resembling somnolence, the circulation and respiration gradually failing.

Since a variation of more than one or two degrees in the temperature of our bodies interferes with the vital activities of the controlling tissue in the *nervous* centres, it is of course of the utmost importance that adequate means for the nice regulation of the mean temperature of our bodies should exist.

The temperature of an animal's body must depend on the relations existing between the amount of heat generated in the tissues and organs and the amount allowed to escape at the surface, and these must closely correspond in order that the heat of the body remain uniform. Both these factors are found to be very variable. Every increase in the activity of the muscles, liver, &c., causes a greater production of heat, while a fall in external temperature or increase in the moisture of the air causes a greater escape of heat from the surface.

The maintenance of uniform temperature may then be accomplished by (1) variations in the heat income, so arranged as to make up for the irregularities of expenditure, or (2) variations in the loss to compensate for the differences of heat generated. Since the temperature and moisture of our surroundings are constantly varying between tolerably wide limits, the amount of heat given off by our bodies must vary greatly at different times. In cold damp weather a great quantity of heat is lost in comparison with that which escapes from the body when the air is dry and warm. If the heat generated had to make up for the changes in the heat lost, one would expect to find a correspondingly great difference in the amount of heat generated at different times of the year, and no doubt we have some evidence in the keener appetite and consequent use of more fuel, and the natural tendency to active muscular exertion during cold weather, to show that a greater amount of combustion does take place in winter than in warm summer weather. If the preservation of a uniform body temperature depended upon the variations in the amount of income exactly following those of the expenditure, we should find it impossible to set our muscular or glandular tissues in action except when the external temperature were such as would enable us easily to get rid of the increased heat following their activity. It certainly would appear that the general tissue combustion, as measured by the amount of CO_2 given off, does increase when we are placed in colder surroundings—such as a cold bath; still, as will presently appear, it is probable that the variations in heat-income have but little regulating influence on the body temperature, and if they have any we are certainly ignorant of the manner in which such influence is carried out.

On the other hand, we know that the amount of *heat-expenditure may* be varied by mechanisms which are almost *self-regulating*. It has already been stated that the great majority of the heat is lost by the parts in contact with the air, namely, the skin and air passages. In these places the warm blood is exposed to the cool air, and therefore loses much of its heat by radiation, conduction, and evaporation. It is obvious that the greater the quantity of blood thus exposed for cooling, the greater will be the amount of heat lost in a given time by the body as a whole.

If we review the circumstances which tend to interfere with the uniformity of the temperature of the body, we shall see that each one is accompanied by certain physiological actions which tend to compensate for the disturbing influences.

The chief common events tending to make our temperature exceed or fall short of its normal standard may be enumerated as follows, and the explanation of their modes of compensation will at the same time be given :—

COMPENSATION FOR INTERNAL VARIATIONS.

A casual increase in the heat income may be induced by any increased chemical activity in the tissues, notably the action of the muscles and large glands. The moment this increased heat is communicated to the blood, the warm blood brings about the following results (partly through the stimulation of certain nerve centres) :— (*a.*) An acceleration of respiratory movement, which increases the amount of cold air to be warmed and saturated with moisture by the air passages, and thus facilitates the escape of the surplus caloric. (*b.*) Relaxation of the cutaneous arterioles, so that a greater quantity of blood is exposed to the cooling influence of the air. (*c.*) Greater rapidity of the heart-beat, by which a greater quantity of blood is supplied to the air passages and to the surface vessels. (*d.*) And commonly an increase in the amount of sweat poured out on the surface, affording opportunity for greater surface evaporation. As an example of these points may be mentioned active muscular exercise, which daily experience shows us is always accompanied by quick breathing, rapid heart's action, and a moist skin. The increased production of heat in fever gives rise to the same results, with the exception of the secretion of the sweat, the want of the secretion (probably owing to the toxic inhibition of the special nerve mechanisms of the glands) is a deficiency in the heat-regulating arrangements, which has much to do with the abnormally high temperature of the disease.

When a lesser quantity of heat is produced, owing to inactivity of the heat-producing tissues, the reverse of these events takes place, namely, the respiration and heart's action are slow, the skin is pale and dry, so that little heat can escape.

COMPENSATION FOR EXTERNAL VARIATIONS OF TEMPERATURE.

When the temperature of the air rises much above the average, the escape of heat is correspondingly hindered; and when the general body temperature begins to rise by this retention of caloric, we have the sequence of events detailed in the last paragraph as being caused by excessive production of heat. But before the blood can become warmer by the influence of the increased external temperature, the warm air, by stimulating the skin, brings about certain changes independent of the body temperature which satisfactorily check the tendency to an abnormal rise. This can be shown by the local application of external heat, by means of which (*a*) a rush of blood to the skin, and (*b*) copious sweat secretion may be induced in a part. This is brought about by impulses sent directly from the skin to the centres regulating the vasomotor and secretory mechanisms, and thus causing vascular dilatation and secretive activity. If only a part be warmed, only a local effort is made to cool that part, and this has but little influence on the general body temperature.

When, however, the atmosphere becomes very warm, all the cutaneous vessels dilate simultaneously, and the escape of heat is greatly increased; while, at the same time, so much blood being occupied in circulating through the skin the deeper—heat-producing—tissues are supplied with less blood, and therefore generate a lesser quantity of heat. Thus a marked rise in the external temperature, which at first sight would seem to impede the escape of heat from the body, really facilitates it, by causing, through the vascular and glandular nerve mechanisms of the skin, a greater exposure of the blood to the cooler air, and a greater quantity of moisture to be evaporated from the warm skin. When the temperature of the air reaches that of the body, then the only way of disposing of the heat generated in the body is by evaporation, for radiation and conduction become impossible. In animals like man, whose cutaneous moisture is so great, external heat seldom causes marked change in the rate of breathing, but in animals whose cutaneous secretion is limited, external heat distinctly affects their respiratory movements, as may be seen by the panting of a dog on a very warm day, even when the animal is at rest.

Almost more important than facilitating the escape of heat in *very warm* weather, are the arrangements for preventing its loss when *the surroundings* are unusually cold. In this case the cold acting as a stimulus to the vaso-constrictor nerve agencies of the skin causes the blood to retire from the surface and fill the deeper organs, where more heat is produced. This bloodless skin and the underlying fat then act as a non-conducting layer or boundary protecting the warm blood from the cooling exposure. At the same time the secretion of the sweat is checked by a special nerve mechanism. Here, too, the cold air, which would soon rob the moist surface of its caloric, checks the secretion and thereby nullifies its effects in this direction, and enables the body to remain at the normal standard temperature.

The chief factors that regulate the body temperature belong then to the expenditure department, and may be said to be—(*a*) variation in the quantity of blood exposed to be cooled, and (*b*) variation in the quantity of moisture exposed for evaporation. These regulators have to compensate not only for differences of external temperature, but also for great fluctuations in the amount of heat produced in the tissues.

The regulating power of the skin, etc., appears to be adequate for the perfect maintenance of uniform temperature only within certain limits. When the limits are passed by the rise or fall of the surrounding medium, the preservation, for any great length of time, of a perfectly uniform body temperature becomes impossible. These limits vary very much in different animals, many of which have special coverings protecting them from external influences, and thus retaining their warmth for all their lifetime in a temperature seldom above 0° C. In man the limits vary much, different individuals being differently affected according to many circumstances, *e.g.*, in both extremes of age the limits are narrowed. It would appear that for about 10° C. above and below the body temperature our skin-regulating mechanisms are adequate, but beyond these limits external changes affect our general temperature, and if continued become injurious. Of course by imitating with clothing the natural protection with which some animals are endowed we can aid the normal regulating factors, and bear much greater extremes of temperature with safety or even comfort.

It surprises many people to hear that their bodies are always at the same temperature, no matter how hot or cold they feel, but, practically, this is the case, for our sensations of being hot or cold mean simply this: when we feel hot our cutaneous vessels are full of warm blood, and this communicates to the cutaneous nerve terminals—the sensory nerves—the sensation of general warmth. On the other hand, when the cutaneous vessels are empty, the sensory nerves are directly affected by the cold of the external air. Since the full or empty state of the vessels of the skin depends generally on the heat or cold of the air, we commonly speak of *its* being cold and *ourselves* being cold as synonymous terms. But we can make ourselves warm by violent exercise even on a frosty day, because we generate so much heat by muscular action that the cutaneous vessels have to be dilated in order to get rid of the surplus, and thereby regulate our body temperature, and thus we have the sensation of being warm. Our feelings when we say we are warm or cold simply depend upon our cutaneous vessels being full or empty of warm blood.

The local appreciation of differences of temperature will be discussed under the sense of Touch.

CHAPTER XXV.

CONTRACTILE TISSUES.

In the lower forms of organisms the motions executed by protoplasm suffice for all their requirements. Thus the amœba manages to pass through its entire lifetime with no other kind of motion at its disposal but the flowing circulation and the budding out of its soft protoplasm. A vast number of minute organisms depend wholly upon the protoplasmic stream and the twitching of cilia for their digestive and progressive movements. Before we leave the class of animals which never pass beyond the unicellular stage, we find, however, examples in which a portion of their protoplasm is specially adapted to the performance of sudden and rapid motions. The protoplasm so modified in function deserves the name of contractile material. Thus, though the protoplasm which lies within the stalk of the bell animalcule is morphologically undifferentiated, it can contract with such rapidity that the eye cannot follow the motion.

As we ascend in the scale of animal life, the necessity of having motions of varied rapidity and duration at the command of the animal becomes more and more urgent, and so we find not only one, but several kinds of tissue specially adapted for carrying out motions of different rate and duration.

As a general rule the more rapid the contraction it performs the more the tissue differs from the original type of protoplasm ; and the slower and more persistent the contraction, the more the tissue elements resemble protoplasmic cells. Thus, in the minute blood vessels, as we have seen, a very prolonged form of contraction, only varied by partial relaxations, is the rule, and gives rise to the tone of the arterioles, and the contractile elements differ but little from ordinary protoplasmic cells. The intestinal movements are rapid compared with those of the arterial muscles, and in them we find a thin, elongated form of muscle cell. In the heart a forcible and quick contraction takes place, which, however, is slow when compared with the sudden jerk of a single spasm of a skeletal muscle, and we find its texture is different, being a form intermediate between the slow-contracting smooth muscle and the quick-contracting striated skeletal muscle.

By borrowing examples from the lower animals, this parallelism of structural differentiation and increase of functional energy can be more perfectly demonstrated, and we can make out a gradual scale of increasingly rapid motion corresponding with greater complexity of structure.

The contractile tissues of the human body show many varieties both of functional and structural differentiation.

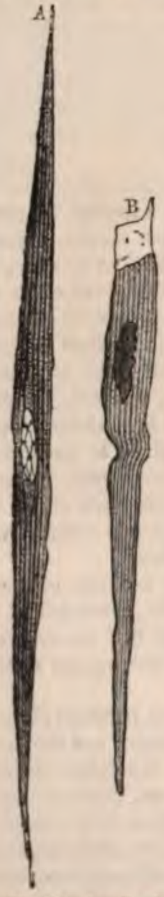


Fig. 177.—Muscle cells, showing different condition of the protoplasm of the *cell and nucleus.*

Histology of Muscle.

The term muscle includes the textures in which the protoplasm is specially differentiated for purposes of contraction.

The muscle tissues of the higher animals may be divided into two classes; 1. non-striated or smooth, and 2. striated, in which again there are some slight variations.

The *unstriated muscle tissue* is that in which the elements are most like contractile protoplasmic cells, and have so far retained the typical form as to be easily recognisable as cells when separated one from the other. These cells are more or less elongated, flattened, homogeneous elements with a single, long, rod-like nucleus and no cell wall. They are tightly cemented together by a tough elastic substance, so that their tapering extremities fit closely together and form commonly a dense mass or sheet. Sometimes they branch more or less regularly, and then are arranged in net-works.

These cells vary greatly in size as well as in the relation of their length to their width, in some places deserving the name fibres, or fibre-cells, and in others being only elongated cells.

The striated muscle tissue is that which is found in the voluntary skeletal muscles and in the tissue of the heart, and therefore forms the large proportion of the animal, and is known as the flesh. The flesh can by judicious dissection easily be divided into single parts called muscles, each of which contains many other tissues and is so attached as to carry on certain movements, and may, therefore, be regarded as an organ.

Such a muscle is enclosed in a sheath of connective tissue from which, sheet-like partitions or septa pass into the mass of the muscle and divide it into bundles of fibres, which they enclose. These septa also act as the bed in which the vessels and nerves lie.

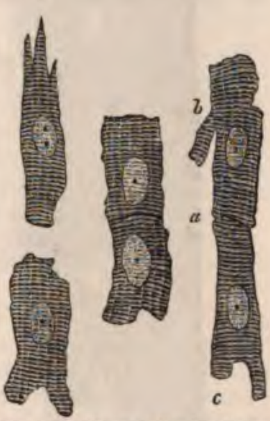


Fig. 178.—Short ,striated cells of the heart muscle, separated one showing the truncated (*a*), or divided (*c*) ends, and branches (*b*).

The bundles of fibres of skeletal muscle vary much in size, giving a coarse or fine grain in different muscles; they are composed of a greater or less number of fibres, which lying side by side run parallel one to the other. The single fibres of striated muscle vary in length, sometimes reaching 4—5 cm. (2 inches), but being on an average much shorter, so that they only extend the entire length of a muscle in the case of very short muscles. In long muscles their tapering points are made to correspond with those of other fibres to which they are firmly attached. The soft fibres are pressed by juxtaposition into prismatic forms, so that in a fresh condition they appear polygonal in transverse section. When freed from all pressure or traction they become cylindrical and the transverse striation of the contractile substance appears regular, and is easily recognised.

Each fibre consists of a delicate case of thin, elastic, homogeneous membrane, forming a sheath called sarcolemma, within which the essential contractile substance is enclosed. The soft contractile substance completely fills and distends the elastic sarcolemma, so that when the latter is broken its contents bulge out or escape. After death, particularly if preserved in weak acid (HCl), the striation becomes more marked, and the dead and now rigid contractile substance can be easily broken up into transverse plates or discs.

Besides the transverse striation a longitudinal marking can be seen in the *muscle fibre which* indicates the subdivision of the contractile substance into thin threads called primitive fibrillæ. Each primitive fibril shows a transverse marking, corresponding with the transverse striation, which divides the fibrils into short blocks called sarcous, or muscle elements. These markings, as well as the transverse striations of the muscle fibre in general, depend on different parts of the contractile substance having different powers of refraction, which give the appearance of dark and light bands.

In the muscle fibre are found long granular masses like protoplasm; these are the nuclei of the contractile substance. They must not be confounded with the nuclei of the sarcolemma, which are much more numerous along the edge of the fibre, or with the other short nuclei seen in such numbers between the fibres, which indicate the position of the capillary vessels.

It is stated that each striated muscle fibre has a nerve fibre passing directly into it, but the exact details of the mode of union in mammalia are not yet satisfactorily made out.

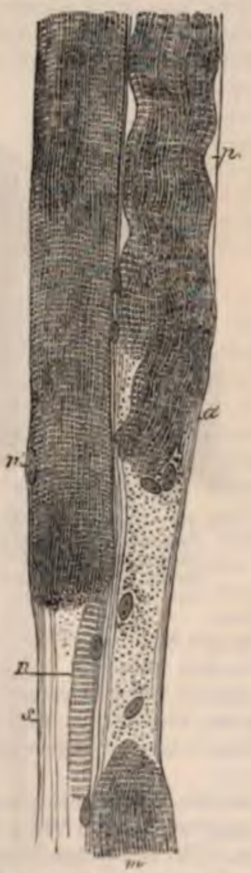


Fig. 179.—Two fibres of striated muscle, in which the contractile substance (m) has been ruptured and separated from the sarcolemma (a) and (s); (p) space under sarcolemma. (Ranvier.)

Properties of Muscle in the Passive State.

Consistence.—The contractile substance of muscle is so soft as to deserve rather the name fluid than solid; it will not drop as a liquid, but its separated parts will flow together again like a half-melted jelly. In this respect it resembles the protoplasm of elementary organisms, the buds from which are so soft that they can unite around foreign bodies, and yet have sufficient consistence to distinguish them from fluid.

Chemical composition.—The chemical composition of the contractile substance of muscle in the living state is not accurately known. The death of the tissue is accompanied by certain changes of a chemical nature which give rise to a kind of coagulation, resulting in the formation of two substances, viz., *muscle serum* and *muscle clot* or *myosin.* This coagulation can be postponed almost indefinitely in the contractile substance of the muscles of cold-blooded animals, by keeping the muscle after its removal at about 5° C. In this way a pale yellow, opalescent, alkaline juice may be pressed out of the muscle and separated on a cold filter. This substance turns to a jelly at freezing point, and on being allowed to come to the ordinary temperature of the room it passes through the stages of coagulation seen in the contractile substance of dead muscle, and gives the same fluid serum and clot of myosin. Since a frog's muscle can be frozen and thawed without the tissue being killed, it is supposed that the thick juice is really the contractile substance, and it has been called *muscle plasma.*

The coagulation of muscle plasma reminds us in many ways of the clotting of the blood plasma, but the muscle-clot, or myosin, which is gelatinous and not in threads like fibrin, is a globulin, and is soluble in 10 per cent. solution of salt. It is readily changed into syntonin or acid albumin, and forms the preponderant albuminous substance of muscle.

The serum of dead muscle has a distinctly acid reaction, and contains three distinct albuminous bodies coagulating at different temperatures, one of which is serum albumin, and another a derived albumin, potassium-albumin. The serum of muscle also contains: (1.) Kreatin, kreatinin, xanthin, &c. (2.) Hæmoglobin. (3.) Grape sugar, muscle sugar, or inosit, and glycogen. (4.) Sarcolactic acid made from the inosit by fermentation. (5.) Carbonic acid. (6). Potassium salts; and (7.) 75 per cent. of water. Traces of pepsin and other ferments have also been found.

Chemical change.—In the state of rest a certain amount of chemical change constantly goes on, by which oxygen is taken from the hæmoglobin of the blood in the capillaries, and carbonic acid is given up to the blood. These changes seem necessary for the nutrition, and therefore the preservation of the life and active powers of the tissue, because if a muscle after removal be placed in an atmosphere free from oxygen, it soon loses its chief vital character, viz., its irritability.

Elasticity.—Striated muscle is easily stretched, and, if the extension be not carried too far, recovers very completely its original length. We say then that the elasticity of muscle is small or weak, but very perfect. When a muscle is stretched to a given extent by a weight—say of 1 gramme—if another gramme be then added, it will not stretch the muscle so much as the first did; and so on if repeated gramme weights be added one after the other, each succeeding gramme will cause less extension of the muscle than the previous one; so that the more a muscle is stretched the more force is required to stretch it to the given extent, or, in other words, the elastic force of muscle increases with its extension.

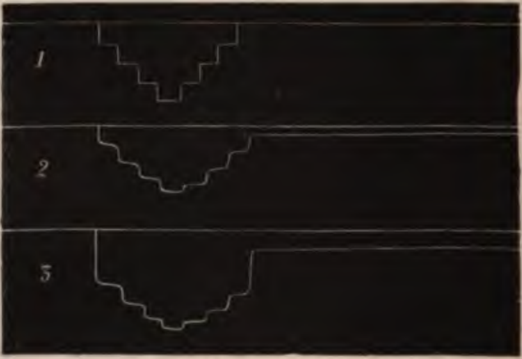


Fig. 180.—1. Shows graphically the amount of extension caused by equal weight increments applied to a steel spring.
2. Shows graphically the amount of extension caused by equal weight increments applied to an india-rubber band.
3. The same applied to a frog's muscle. Showing the decreasing increments of extension; the gradual continuing stretching and the failure to return to the abscissa when the weight is removed.

If a tracing be drawn showing the extending effect of a series of equal weights attached to a fresh muscle, it will be found that a great difference exists between it and a similar record drawn by inorganic bodies or an elastic band of rubber.

When a weight is applied to a muscle, it does not immediately stretch to the full extent the weight is capable of effecting, but a certain time, which varies with circumstances, is required for its complete extension. The rate of extension is at first rapid, then slower, until it ceases. As a muscle loses its powers of contraction from fatigue, it becomes more easily extended. Dead muscle has a greater but less perfect elasticity than living, *i.e.*, it requires greater force to stretch it, but does not return so perfectly to its former shape. The importance of the elastic property of muscle in the movements of the body is noteworthy. The muscles are always in some degree on the stretch (as can be seen in a fractured patella, the fragments of which remain far apart and cause the surgeon much anxiety), and brace the bones together like a series of springs, the various skeletal muscles being so arranged as to stretch others by their contraction. When one muscle—for example, the biceps—contracts, it finds an elastic antagonist already tense ; this it has to stretch as it shortens. The triceps thus acts as a weak spring, opposing the biceps, and it gently returns to its natural length when the contraction of the biceps ceases. By their mere elasticity the muscles are kept tense and ready for action, and have to act against a gentle spring-like resistance, so that the motions are even, and there is no jerking, as would occur if the attachments of the inactive muscles were allowed to become slack.

Electric Phenomena.—In a living muscle electric currents may be detected, having a definite direction, and certain relations to the vitality of the tissue. As they seem to be invariably present in a passive muscle they have been called *natural muscle currents.*

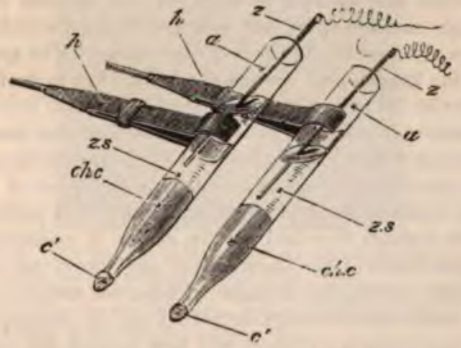


Fig. 181.—Non-polarisable Electrodes. The glass tubes (*a a*) contain sulphate of zinc solution (*z. s*), into which well amalgamated zinc rods dip. The lower extremity is plugged with china clay (*ch. c*), which protrudes at (*c'*) the point. The tubes can be moved in the holders (*h h*), so as to be brought accurately into contact with the muscle. (Foster.)

They are generally studied in the muscles of cold-blooded animals after removal from the body. The muscle is spoken of as if it were a cylinder with longitudinal and transverse surfaces corresponding to its natural surface and its cut extremities. In such a block of frog's muscle the measurement of the electric currents requires considerable care, because they are so difficult to detect that a most sensitive galvanometer must be used; and such an instrument can easily be disturbed by currents due to bringing metal electrodes into contact with the moist saline tissues. Specially constructed electrodes must be used to avoid these currents of polarisation taking place in the terminals touching the muscle. These are called *non-polarisable electrodes*, and may be made on the following plan:—Some innocuous material moistened in saline solution (·65 per cent.) is brought into direct contact with the muscle, and, by means of saturated solution of zinc sulphate, into electrical connection with amalgamated zinc terminals from the galvanometer. Thus the muscle is not injured, and the zinc solution prevents the metal terminals from producing adventitious currents.

Small glass tubes drawn to a point, the opening of which is plugged with moist china clay, make a suitable receptacle for the zinc solution, or, instead of the china clay, a camel-hair brush set in plaster of Paris may be used to keep the zinc solution in the tube, and the hair moistened in salt solution forms a suitable point of contact with the muscle. If a pair of such electrodes be applied to the middle of the longitudinal surface at (*e*) (fig. 182), and of the transverse surface at (*p*) respectively, and then be brought into connection with a delicate galvanometer, it is found that a current passes through the galvanometer from the longitudinal to the transverse surface. A current in this direction can be detected in any piece of muscle, no matter how much it be divided longitudinally, and probably would be found in a single fibre had we the means of examining it. The nearer to the centre of the longitudinal and transverse sections the electrodes are placed, the stronger will be the current received by them. If both the electrodes be placed on the longitudinal or on the transverse surfaces a current will pass through the galvanometer from that electrode nearer the middle of the longitudinal section (called the equator of the muscle cylinder) to the electrode nearer the centre of the transverse section (pole of muscle cylinder). If the electrodes be placed equidistant from the poles or from the equator no current can be detected.

The central part of the longitudinal surface of a piece of muscle is then positive, compared with the central part of the extremities or transverse sections. And between these parts, the equator and poles of the muscle cylinder, where the difference is most marked, are various gradations, so that any point near the equator is positive when compared with one near the poles.

There is, then, a current passing through the substance of the piece of muscle from both the transverse sections or extremities of the muscle block to the middle of the longitudinal surface, whether it be a cut surface (longitudinal section) or the natural surface of the muscle. This is called the *muscle current*, or sometimes natural muscle current.

If the cylinder in the accompanying figure be taken to represent a block of muscle, *e* would correspond to the equator, and *p* to the poles, and the arrowheads show the direction of the currents passing through the galvanometer, the thickness of the lines indicating their force. The dotted lines *o* are connected with points where the electro-motive force is equal, and therefore no current exists.

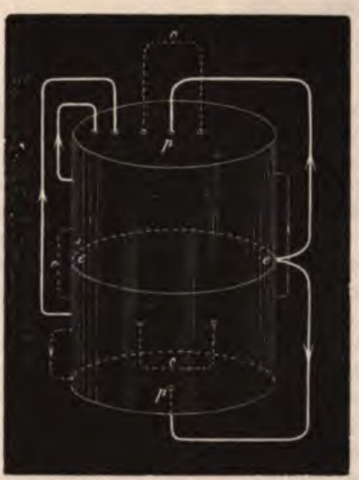


Fig. 182.—Diagram to illustrate the currents in muscle.
(*e*) Equator, corresponds to the centre of the muscle.
(*p*) Polar regions of cylinder representing the extremities of the muscle.
The arrow heads show the direction of the surface currents, and the thickness of lines indicates the strength of the currents. (After Fick.)

The electro-motive force of the muscle-current in a frog's gracilis has been estimated to be about ·05—·08 of a Daniell cell. It gradually diminishes as the muscle loses its vital properties, and is also reduced by fatigue. The electromotive force rises with the temperature from 5° C. until a maximum is reached at about the body temperature of mammals.

These muscle-currents are very weak if the uninjured muscle be examined *in situ*, the tendon being used as the transverse section; they soon become more marked after the exposure of the muscle, and if the tendon be injured they appear at once in almost full force. In animals quite inactive from cold the muscles naturally are but slowly altered by exposure, &c., and the muscle-currents do not appear for a considerable time, which is shortened on elevating the temperature. It has, therefore, been supposed that in the perfectly normal state of a living animal there are no muscle-currents so long as the muscle remains in the passive state.

ACTIVE STATE OF MUSCLE.

A muscle is capable of changing from the passive elongated condition, the properties of which have just been described, into a state of contraction or activity. Besides the change in form, obvious in the contracted state of the muscle, its chemical, elastic, electric, and thermic properties are altered. The capability of passing into this active condition is spoken of as the *irritability* of muscle. This is directly dependent upon its chemical condition, and therefore related to its nutrition and to the amount of activity recently exerted, which, it will hereafter appear, changes its chemical state.

Under ordinary circumstances, during life, the muscles change from the passive state into that of contraction in response to certain impulses communicated to them by nerves, which carry impressions from the brain or spinal cord to the skeletal muscles. The influence of the will is, then, the common stimulus which excites most skeletal muscles to action. But we find that there are many other influences which, when applied to a muscle, can also bring about the same change. These influences are called *stimuli*.

We commonly utilise the nerve belonging to a muscle in order to throw it into the contracted state, but the great majority of stimuli can bring about the change when applied to the muscle directly. Since the nerves branch in the substance of the muscle, and are distributed to the individual fibres, it might, as has been argued, be the stimulation of the terminal nerve ramifications that brings about the contraction, even when the stimulus is applied to the muscle directly, for the nerves of course would be affected by the stimulus applied to the muscle. That muscles can be stimulated without the intervention of nerves is satisfactorily proved by the following facts :—1. Some parts of muscles, such as the lower end of the sartorius, and many muscular structures which have no nerve *terminals* in them, respond energetically to all kinds of muscle *stimuli*. 2. There are some substances which act as stimuli when applied directly to muscle, but have no such effect upon nerves, viz., ammonia. 3. For some time after the nerve has ceased to react, on account of its dying after removal from the body, the attached muscle will be found quite irritable if directly stimulated. 4. The arrow-poison, Curara, has the extraordinary effect of paralysing the nerve terminals, so that the strongest stimulation of the nerve calls forth no muscle contraction. If the muscles in an animal under the influence of this poison be stimulated directly, they respond with a contraction.

This separation of muscles from nerves would appear rather artificial, and antagonistic to the teachings of the development of these tissues, both in the ascending scale of the animal kingdom and in the individual.

MUSCLE-STIMULI.

The circumstances which call forth muscle contraction may be enumerated thus :—

1. *Mechanical Stimulation.*—Any sudden blow, pinch, &c., of a living muscle causes a momentary contraction, which rapidly passes off when the irritation is removed.

2. *Thermic Stimulation.*—If a frog's muscle be warmed to over 30° C. it will begin to contract, and before it reaches 40° C. the muscle will pass into a condition known as heat rigor, which will be mentioned presently. If the temperature of a muscle be reduced below 0°C. it shortens before it becomes frozen.

3. *Chemical Stimulation.*—A number of chemical compounds also act as stimuli when they are applied to the transverse section of a divided muscle. Among these may be named—(1) the mineral acids (HCl, ·1 per cent.) and many organic acids ; (2) salts of iron, zinc, silver, copper, and lead ; (3) the neutral salts of the alkalies of a certain strength ; (4) weak glycerine and weak lactic acid, which only excite nerves when concentrated ; (5) bile also is said to stimulate muscle in much weaker solutions than it will nerve fibres.

4.—*Electric Stimulation.*—Electricity is the most convenient form of stimulation, because we can accurately regulate the force of the stimulus. The occurrence of any variation in the intensity of an electric current passing through a muscle causes it to contract. The sudden increase or decrease in the strength of a current acts as a stimulus, but a current of exactly even intensity may be made to pass through a muscle without exciting any contraction. The common method employed is that of opening or closing a circuit of which the muscle forms a part, so as to make or break the current ;

and thus a variation of intensity, equal to the entire strength of the current used, takes place in the muscle, and acts as a stimulus.

The irritability of muscle substance is not so great as that of the motor nerves, that is to say, a slight stimulus will make the muscle contract when applied to its nerve, while the same stimulus will have no effect if applied to the muscle directly. In experimenting on the contraction of muscle, as already stated, the intervention of the nerve is commonly used, the stimulus, by means of an electric current applied to the nerve, being more conveniently and completely distributed to the muscle than when applied directly.

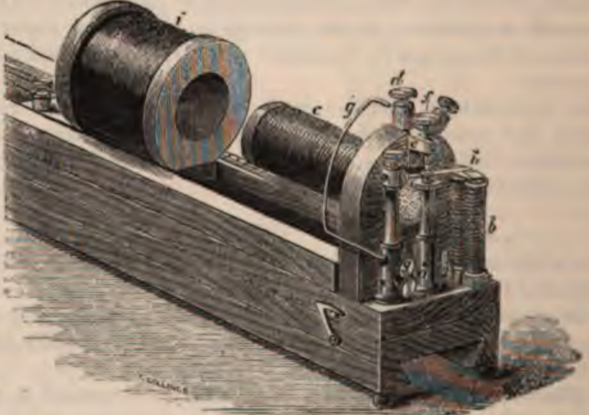


Fig. 183.—Du Bois Reymond's Inductorium with Magnetic Interrupter.

c. Primary coil through which the primary, *inducing*, current passes, on its way through the electro-magnet (*b*).

i. Secondary coil, which can be moved nearer to or further from the primary coil (*c*), thereby allowing a stronger or weaker current to be induced in it. This *induced* current is the stimulating one.

b. Electro-magnet, which on receiving the current breaks the contact in the circuit of the primary coil by pulling down the iron hammer (*h*), and separating the spring from the screw of *e.* When it brings the spring in contact with the point of the pillar (*a*), it also demagnetises itself by "short-circuiting" the battery.

When tetanus is to be produced, the wires from the battery are to be connected with *g* and *d.*

When a single contraction is required, the magnetic interrupter is cut out by shifting the wire from *a* to the binding screw to the right of *f.*

The current of a battery may be used to stimulate a muscle, but *an induced* current is more commonly employed on account of the greater efficacy of its action. The instrument in ordinary use in physiological laboratories is Du Bois-Reymond's inductorium, in which the strength of the stimulus can be reduced by removal of the secondary coil, and which is supplied with a magnetic interrupter, by means of which repeated stimuli may be given. (See Fig. 183.)

CHANGES OCCURRING IN MUSCLE ON ITS ENTERING THE ACTIVE STATE.

Changes in Structure.—The examination of muscle with the microscope during its contraction is attended with considerable difficulty, and in the higher animals has not led to satisfactory results. In the muscles of insects, where the differentiation of the contractile substance is more complicated, certain changes can be observed. The fibres, and even the fibrillæ within them, can easily enough be seen to undergo changes in form corresponding to those of the entire muscle, namely, increase in thickness and diminution in length. A change in the position and relative size of the singly and doubly refracting portions of the muscle element has been described, and some authors state that the latter increases at the expense of the former after an intermediate period in which the two substances seem fused together.

Chemical Changes.—During the contracted condition the chemical changes which go on in passive muscle are intensified, and certain new chemical decompositions arise of which, however, not much is known.

Active muscle takes up more oxygen than muscle at rest, as is shown by the facts that, during active muscular exercise, more oxygen enters the body by respiration, and the blood leaving active muscles is poorer in oxygen than when the same muscles are passive. This absorption of oxygen cannot be detected in a muscle cut out of the body, nor is any supply of oxygen necessary for a contraction of such a muscle, since a frog's muscle will contract in an atmosphere containing no oxygen. From this it would appear that a certain ready store of oxygen must exist in some chemical constituent of the muscle substance, and it is possible that some chemical compound, which is constantly renewed by the blood existing in the muscle, is its normal source of oxygen, and not the oxy-hæmoglobin of the blood.

The amount of CO_2 given off by a muscle increases in its state of activity, as may be seen by the greater elimination from the lungs during active muscular exercise, and by the fact that the venous blood of a *limb, when* the muscles are contracted, contains more

CO_2 than when they are relaxed. The increase of CO_2 can also be detected in a muscle removed from the body and kept in a state of contraction. Moreover, this increase in the formation of CO_2 in a muscle takes place whether there is a new supply of oxygen given to it or not, and the quantity of CO_2 given off always greatly exceeds the quantity of oxygen that is used up. So that it is not exclusively if at all from the newly-supplied oxygen that the CO_2 is produced.

Muscle tissue, when passive, is neutral or faintly alkaline; during contraction, however, it becomes distinctly acid. The litmus which it changes from blue to red is permanently altered, and we can, therefore, conclude that CO_2 is not the only acid that makes its appearance. The other acid is *sarcolactic acid*, which is constantly present in muscle after prolonged contraction, and varies in amount in proportion to the degree of activity the muscle has undergone. It therefore varies directly with the CO_2, which would seem to suggest a relationship between the origin of the two acids.

The amount of glycogen and grape sugar is said to diminish in muscle during its activity, and it is stated that sarcolactic acid can be produced from these carbo-hydrates by the action of certain ferments.

Active muscle contains more substances that can be extracted by alcohol and less that are soluble in water than passive muscle.

The chemical changes which take place during muscle contraction are probably the result of a decomposition of some carbo-hydrates, in which the albuminous substances do not take any part that requires their own destruction. This seems supported by the fact that the increased gas exchange in muscle during active exercise can be recognised in a corresponding change in the gas exchange in pulmonary respiration; and, moreover, there seems no relation between muscular labour and the amount of nitrogenous waste, as estimated by the urea elimination, which one would expect if muscular activities were the outcome of a decomposition of the nitrogenous (albuminous) parts of the muscle substance.

The chemical changes which are commonly said to take place in muscle during its contraction are :—

1. The contractile substance, which is normally neutral or faintly alkaline, becomes acid in reaction owing to the formation of sarcolactic acid.

2. More oxygen is taken up from the blood than in the muscle at rest. This using up of oxygen occurs also in the isolated muscle, and its amount appears to be independent of the blood supply.

3. The extractives soluble in water decrease, those soluble in alcohol increase.

4. A greater amount of CO_2 is given off, both in the isolated muscle as well as in the muscles in the body, and the change in the quantity of CO_2 has no exact relation to that of the oxygen used.

5. A diminution is said to occur in the contained glycogen, and certainly prolonged inactivity causes an increase in the amount of glycogen.

6. A peculiar muscle-sugar makes its appearance.

Change in Elasticity.—The elasticity of a muscle during its state of contraction is less than when it is in the passive state. That is to say, that a given weight will extend the same muscle more if attached to it while contracted (as in tetanus) than when it is relaxed. The contracted muscle is then more extensible. If, then, a weight which is just over the maximum load the muscle can lift, be hung from it and the muscle then stimulated, it should become extended, because the change to the active state lessens its elastic power, while it cannot contract, being over-weighted.

Electrical Changes.—If a muscle, in connection with a galvanometer so as to show the natural current, be stimulated by means of the nerves, a marked change occurs in the current. The galvanometric needle swings towards zero, showing that the current is weakened or destroyed. This is called the *negative variation* of the muscle current which initiates the change to the active condition. When the muscle *receives but* a momentary stimulus so as only to give a

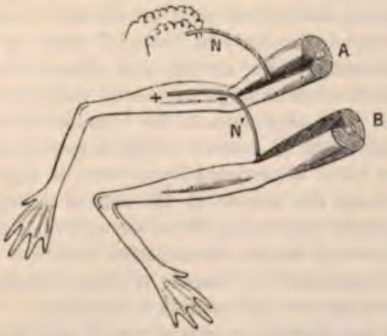


Fig. 184.—Diagram illustrating the arrangement in the Rheoscopic Frog.

A = *stimulating* limb. B = *stimulated* limb. The current from the electrodes passes into nerve (N) of stimulating limb (A), causing its gastrocnemius to contract. Whereupon the negative variation of the natural current between + and − stimulates the nerve (N′), and excites the muscles of B to action.

single contraction, this negative variation takes place in the current, but, owing to its extremely short duration, the galvanometric needle is prevented by its inertia from following the change. Only the most sensitive and well-regulated instruments show the electric change of a single contraction, but when the muscle is kept contracted by a series of rapidly repeated stimulations then the inertia of the needle is readily overcome. The negative variation of a single contraction can, however, be easily shown on the sensitive animal tissues. For this purpose the nerve of one nerve-muscle preparation* is placed upon the surface of another muscle so as to pass over the middle of the transverse and longitudinal sections. Then the second (stimulating) muscle is made to contract, the negative variation acts as a stimulus to the nerves lying on it, and so the first (stimulated) muscle contracts. Not only does this show the negative variation of a single contraction, but it also demonstrates that the continued (tetanic) contraction produced by repeated stimulation is associated with repeated negative variations. Because the contraction of the stimulated muscle whose nerve lies on the stimulating muscle follows exactly all the variations of the stimulator, and is kept contracted as long as the other is contracted, and, as we shall see presently, the continued contraction can only be brought about by a rapidly repeated series of stimulations, so that the electric condition of the stimulating muscle must undergo a series of variations.

If an isolated part of a muscle be stimulated the contraction passes from that point as a wave to the remainder of the muscle. This contraction wave is preceded by a wave of negative variation which passes along the muscle at the rate of 3 metres per second (the same rate as the contraction wave, see under), lasting at any one point ·003 of a second, so that the negative variation is over before the contraction begins, for the muscle requires a certain time, called the latent period, before it commences to contract.

The origin of the electric currents of muscle will be discussed with nerve-currents, to which the reader is referred (p. 421).

Temperature Change.—Long since it was observed in the human subject that the temperature of muscles rose during their activity. In frogs' muscle a contraction lasting 3 minutes caused an elevation of ·18° C. And a single contraction is said to produce a rise varying from ·001° to ·005° C., according to circumstances.

The production of heat is in proportion to the tension of the muscle. When the muscles are prevented from shortening a greater amount of heat is said to be produced.

---

* By a nerve-muscle preparation is meant a muscle of a frog (commonly the gastrocnemius and the half of the femur to which it is attached) and its nerve which has been carefully separated from other parts and removed from the body.

The amount of heat has also a definite relation to the work performed. Up to a certain point the greater the load a muscle has to move, the greater the heat produced; when this maximum is reached any further increase of the weight causes a falling off in the heat production. Repeated single contractions are said to produce more heat than tetanus kept up for a corresponding time.

The fatigue which follows prolonged activity is accompanied by a diminution in the temperature elevation.

Muscle Contraction.

Change in form.—The most obvious change a muscle undergoes in passing into the active state is its alteration in shape. It becomes shorter and thicker. The actual amount of shortening varies according to circumstances. (*a*) A muscle on the stretch when stimulated will shorten more in proportion than one whose elasticity is not called into play before contraction, so that a weighted muscle shortens more than an unweighted one with the same stimulus. (*b*) The fresher and more irritable a muscle is, the shorter it will become in response to a given stimulus; and, conversely, a muscle which has been some time removed from the body, or is fatigued by prolonged activity, will contract proportionately less. (*c*) Within certain limits, the stronger the stimulus applied the shorter a muscle will become. (*d*) A warm temperature augments the amount of shortening, the amount of contraction of frogs' muscles increasing up to 33° C. A perfectly active frog's muscle shortens to about half its normal length. If much stretched and stimulated with a strong current it may contract nearly to one fourth of its length when extended. Muscles are seldom made up of perfectly parallel fibres, the direction and arrangement varying much in different muscles. The more parallel to the long axis of the muscle the fibres run, the more will the given muscle be able to shorten in proportion to its length.

The thickness of a muscle increases in proportion to its shortening during contraction, so that there is but little change in bulk. It is said, however, to diminish slightly in volume, becoming less than $\frac{1}{1000}$th smaller. This can be shown by making a muscle contract in a bottle filled with weak salt solution so as to exclude all air and to communicate with the atmosphere only by a capillary tube into which the salt solution rises. The slightest decrease in bulk is then shown by the fall of the thin column of fluid in the tube.

Since a muscle loses in elastic force and gains but little in density during contraction the hardness which is communicated to the touch depends on the difference of tension of the semi-fluid contractile substance within the muscle sheath.

THE GRAPHIC METHOD OF RECORDING MUSCLE CONTRACTION.

In order to study the details of the contraction of muscle, the graphic method of recording the motion is applied. The curve may be drawn on an ordinary cylinder moving sufficiently rapidly. Where accurate time measurements are required it is better to use one of the many special forms of instruments, called *myographs*, made for the purpose. The principle of all these instruments is the same; namely, an electric current, which passes through the nerve of a frog's muscle connected with the marking lever, is broken by some mechanism, while the surface is in motion; the exact moment of breaking the contact can be accurately marked off on the recording surface by the lever which draws the muscle curve before the instrument is set in motion. The rate of motion is registered by a curve drawn by a tuning fork of known rate of vibration.

In order that the muscle-nerve preparation may not be injured by the tissues becoming too dry, it is placed in a small glass box, the air of which is kept moist by a damp sponge. This *moist chamber* is used when any living tissue is to be protected from drying.

The first myograph used was a complicated instrument devised by Helmholtz; in which a small glass cylinder is made to rotate rapidly by a heavy weight, and when a certain velocity of rotation is attained, a tooth is thrown out by centrifugal force, which breaks the circuit of the current passing through the nerve of the muscle. The tendon is attached to a balanced lever, at one end of which hangs a rigid style pressed by its own weight against the glass cylinder. When the circuit is broken the muscle contracts, raises the lever, and makes the style draw on the smoked glass cylinder.

Fick introduced a flat recording surface moving by the swing of a pendulum, by which the abscissa is made a segment of a circle, and not a straight line, and the rate varies, so that the different parts of the curve have varying time-values. The curves given in the following wood-cuts are drawn with the *Pendulum Myograph*.

Du Bois-Reymond draws muscle curves on the smoked surface of a small glass plate contained in a frame, which is shot by the force of a spiral spring along tense wires, and on its way breaks the contact. The trigger used for releasing the spring sets a tuning fork at the same time vibrating.

SINGLE CONTRACTION.

In response to a single instantaneous stimulus, such as the making or breaking of an electric current, a muscle gives a momentary twitch or spasm, commonly spoken of as a *single contraction*, which is of so short duration, that without the graphic method of recording the motion we could not appreciate the phases which are seen on the curve.

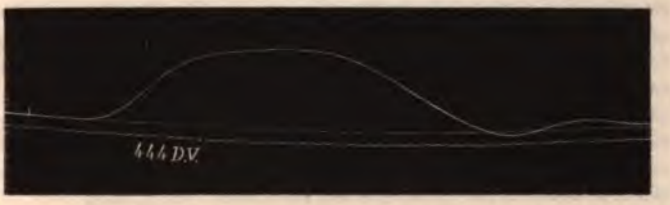


Fig. 185.—Curve drawn by a frog's gastrocnemius on the Pendulum Myograph, below is seen the tuning fork record of the time occupied by the contraction. Parallel to the latter is the abscissa. The little vertical mark at the left shows the moment of stimulation, and the distance from this to the beginning of the rise of the curve gives the latent period, which is followed by the ascent and descent of the lever.

The curve drawn on the recording surface of a pendulum myograph, by such a single contraction, is represented in figure 183. The short vertical stroke on the abscissa or base line is drawn by touching the lever when the muscle is in the uncontracted state, and indicates the time of stimulation. The upper curved line is drawn by the lever and during the contraction of the muscle.

In such a curve the following stages are to be distinguished :—

1. A short period between the moment of stimulation and that at which the lever begins to rise, during which the muscle does not move. This is known as the *latent period.* In the skeletal muscles of the frog this period lasts about ·01 sec.

2. A period during which the lever rises, at first slowly, then more quickly, then again slowly, until it ceases to rise. This stage has been called the period of *rising energy.* It lasts about 0·04 sec.

3. When the highest point is attained the lever commences to fall, at first slowly, then more quickly, and at last slowly. There is then no pause at the height of contraction. The stage of relaxing has been called the period of *falling energy.* It is said to occupy a somewhat longer time than the second period, lasting about $\frac{5}{100}$ sec.

Thus we see that a stimulus occupying an immeasurably short time sets up a *change in the* molecular condition, which taking nearly

$\frac{1}{10}$ sec. to run its course, and requiring $\frac{1}{100}$ sec. before it exhibits any change of form, then in $\frac{4}{100}$ sec. attaining the maximum height of contraction, and without waiting in the contracted condition, spends $\frac{5}{100}$ sec. in relaxing.

The *latent period* which appears in a *single contraction curve* drawn by a muscle stimulated in the usual way, through the medium of a nerve, is not entirely occupied by preparatory changes going on in the substance of the muscle, but a certain part of the time recorded as latent period corresponds to the time required for the transmission of the impulse along the nerve. This may be shown by stimulating first the far end of the nerve and then the muscle itself. In this case two curves will be drawn having different latent periods, that obtained by direct stimulation of the muscle being shorter, and representing the real latent period of the muscle, while the longer one includes the time taken by the impulse to travel along the piece of nerve between the electrodes and the muscle (see p. 420).

The latent period varies much in different kinds of muscle in the same kind of muscle of different animals, and in the same individual muscle under different conditions. As a rule the slow-contracting muscles have a longer latent period. Thus the non-striated slow contracting muscles found in the hollow viscera have a latent period of some seconds. The striated muscles of cold-blooded animals have a longer latency than the same kind of muscle in birds and mammalia. The same gastrocnemius of a frog has a shorter latent period when strongly stimulated, or when its temperature is raised, and *vice versa*.

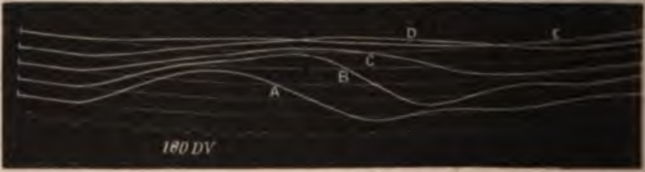


Fig. 186.—Curves drawn by the same muscle in different stages of fatigue—A, when fresh; B, C, D, E, each immediately after the muscle had contracted 200 times. Showing that fatigue causes a low, long contraction.

The latent period is considerably lengthened by fatigue. If the weight be so applied that it does not extend the muscle before contraction, but only bears on it the instant it commences to shorten, the duration of the latent period increases in proportion to the weight the muscle has to lift.

The duration of the single contraction of striated muscle varies in different cases and under varying circumstances. The greatest difference is reached by the muscles found in different kinds of animals. The contraction of some kinds of muscle tissue (non-striated muscle of mollusca, for example) occupies several minutes, and reminds one of the slow movement of protoplasm; while the rapid action of the muscle of the wing of a horsefly occurs 330 times a second. Various gradations between these extremes in the rapidity of muscle contraction may be found in the contractile tissues of different animals. The following table gives the rate of contraction of some insects' muscles, which may help to show the extent of these variations.

Horsefly . .	330 contractions per second.	
Bee . . .	190 ,,	,,
Wasp . . .	110 ,,	,,
Dragon-fly . .	28 ,,	,,
Butterfly . .	9 ,,	,,

Among the vertebrata the duration of the contraction of the skeletal muscles varies considerably according to the habits of the animal. The limb muscles of the tortoise and toad take a very long time to finish their contraction; other muscles of the same animals act more quickly, but do not attain the rapidity of contraction of the skeletal muscles of warm-blooded animals.

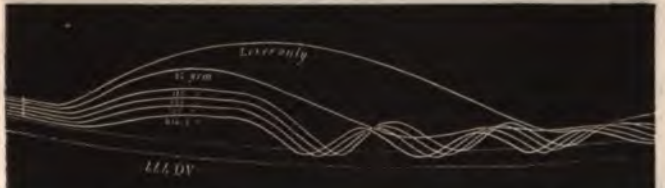


Fig. 187.—Six curves drawn by the same muscle when stretched by different weights Showing that as the weight is increased the latency becomes longer and the contraction less in height and duration.

The duration of a single contraction of the same muscle is also capable of considerable variation. It seems to be lengthened by anything that leads to an accumulation of the chemical products which arise from muscle activity. Hence fatigue or over-stimulation cause a slow contraction (Fig. 186).

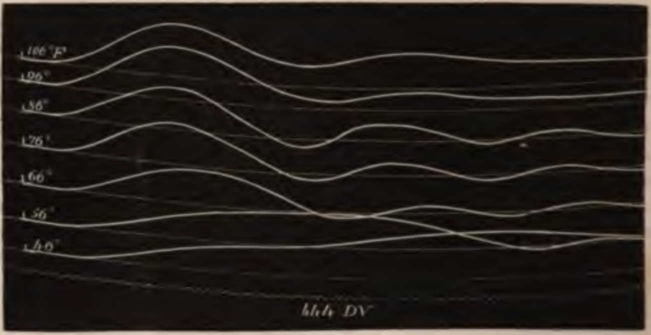


Fig. 188.—Curves drawn by the same muscle at different temperatures. Showing that with elevation of temperature the latency and the contraction become shorter. (The muscle had been previously cooled.)

Moderate increase of temperature greatly shortens the time occupied by the single contraction of any given muscle. Excessive heat causes a state of continued contraction.

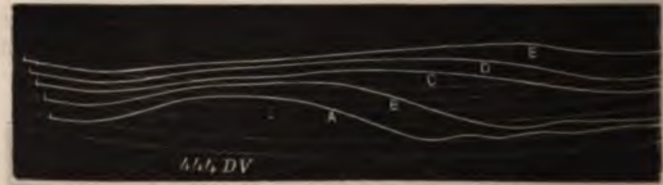


Fig. 189.—Curves drawn by the same muscle while being cooled. Showing that the latency and the contraction become longer as the temperature is reduced.

The reduction of temperature causes a muscle to contract more slowly, and, when extreme, the muscle remains contracted long after the stimulus is removed.

Wave of Contraction.—If one extremity of a long muscle be stimulated without the aid of the nerve (it is best to employ a muscle from a curarised animal), the contraction passes along the muscle from the point of stimulation in a wave which travels at a definite rate of 3—4 metres per sec. in a frog, and 4—5 metres per sec. in a mammal. Reduction of temperature and fading of vital activity cause the velocity of the wave to be lessened, until finally the tissue ceases to conduct; then only a local contraction occurs, severe stimulus causing simply an elevation at the point of contact. This seems analogous to the idio-muscular contraction, which marks the seat of severe mechanical stimulation after the general contraction has ended.

MAXIMUM CONTRACTION.

The extent to which a muscle will contract depends upon the conditions in which it is placed, and varies, as we have seen, with the load, its irritability, the temperature, and the force of the stimulus. A fresh muscle then, at the ordinary temperature with a medium load, will contract more and more as the intensity of the current employed increases. There is a limit to this increase, and with comparatively weak stimulation, an effect is produced which cannot be surpassed by the same muscle, no matter what stimulus be applied. This greatest contraction is the same for all medium stimuli while the muscle is fresh, and is called the *maximum contraction*, being the greatest shortening which can be produced by a single instantaneous stimulus.

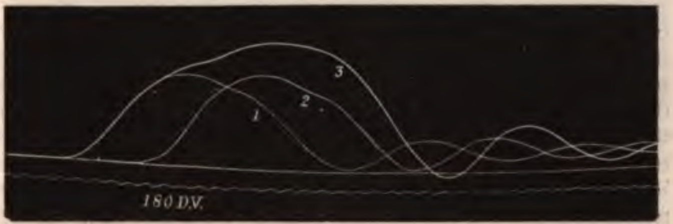


Fig. 190.—Pendulum myograph tracings showing summation.

1. **Curve of maximum contraction drawn by first stimulus, the exact time of application of which is shown by the small up-stroke of the left hand of the base line.**
2. **Maximum contraction resulting from second simple stimulation given at the moment indicated by the other small up-stroke.**
3. **Curve drawn as the result of double stimulation sent in at an interval indicated by the distance between the up-strokes, showing summation of stimulus and consequent increase in contraction over the "maximum contraction."**

Summation.—Each time a muscle receives an induction shock of medium strength it contracts to its maximum. If a second shock be given while the muscle is in the contracted state, a new maximum contraction is added to the extent of the contraction the muscle was in at the moment of the second stimulation, and if stimulated when the lever is at the apex of the curve the sum of the effect produced will be equal to two maximum contractions.

If applied in the middle of the period of the ascent or descent of the lever a second stimulation gives rise to 1½ maximum contractions, and so on, in various parts of the curve, a new maximum curve is produced, arising from the point at which the lever is when the second stimulus is applied (Fig. 190).

During the latent period a second stimulation produces less marked effect, and is difficult to demonstrate, but if the second stimulus come after an interval of more than $\frac{1}{600}$ sec., summation can be appreciated.

This summation of effect also takes place when the stimulus is insufficient to produce a maximum contraction, the succeeding weak stimuli give rise to the same extent of contraction of the already partially contracted muscle, as if it were at its normal length at the time of the second stimulation. The following tracings (Figs. 191—193) show the effects of repeated stimulations applied at the various periods indicated by the numbers on the abscissa line.

TETANUS.

If a series of stimuli be applied one after the other, at intervals equal to about half the duration of a single contraction, a summation of contractions occurs, which results in the accumulation of effect until the muscle has shortened to about one-half of the length it attains during a single contraction, or about one-fourth the normal length of the relaxed muscle; it can then shorten no more no matter how the stimulus be increased in rate or strength. Not having sufficient time between the stimuli it cannot relax, so it remains contracted permanently as long as the stimulus is continued, the various single contractions caused by the repeated shock all being fused together (Fig. 191); but if the interval be more than half the time occupied by a single contraction then the line drawn by the lever will show notches indicating the apices of the fused single contractions (Figs. 192 and 193).

This condition of continuous summation of contractions is called *tetanus*, and in all probability is not only the commonest but the only kind of muscular motion that can be produced by the action of the nerves in obedience to the will. All the actions of our skeletal muscles are then made up of the fusion of many single contractions into tetanus, and such motions as appear too quick for tetanic action are accomplished by the interposition, at a certain moment, of the action of an antagonistic muscle which stops the movement and makes the act extremely rapid.

With from twenty a second to upwards of many hundreds of induced shocks one can produce tetanus in a frog's muscle. The lowest limit of this range is probably about the number of impulses communicated to human muscles by their nerves, since the tone produced by contracting muscle corresponds to the first overtone of a primary note produced by 19·5 vibrations in a second. The number of

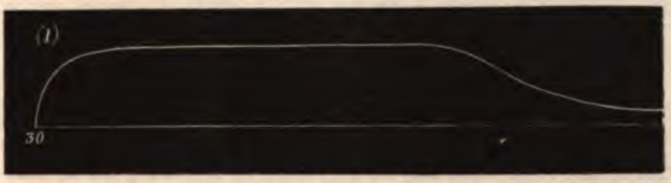


Fig. 191.—Curve of tetanus resulting from 30 stimulations per second, drawn on a drum rotating slowly compared with the motion of the Pendulum Hyograph. The stimulation commences at "30," and ceases just before the lever begins to fall. No trace of the individual contractions of which the tetanus is composed can be recognised.

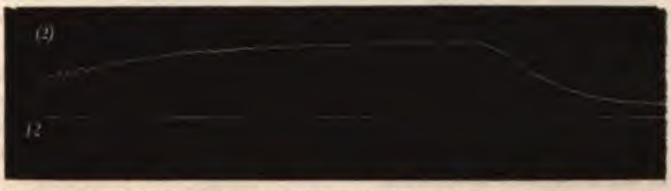


Fig. 192.—Curve of tetanus composed of imperfectly fused contractions resulting from 12 stimulations per second. The serrations on the left of the curve indicate the individual contractions.

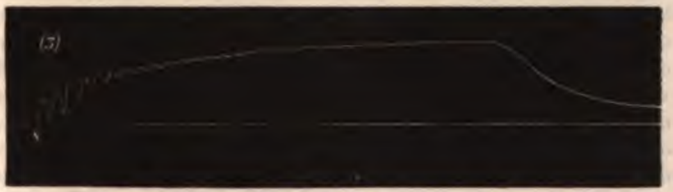


Fig. 193.—Tetanus produced by 8 stimulations per second.
The more perfect fusion of the single contractions shown towards the end of the curve depends on the altered condition of the muscle.

stimuli required varies with the rate of contraction of the muscle employed, the quick contracting bird's muscle requiring 70 per second, while the exceptionally slow-moving tortoise muscle only requires 3 per second. According to some, there is a limit to the number of stimuli which will cause tetanus, 360 per second is named as the maximum for a certain strength of stimulus; with stronger stimuli, even when more frequent, tetanus occurs. It has been shown that many thousand stimuli per second can cause tetanus even with very weak currents. If tetanus be kept up for some seconds, and the stimulation be then suddenly stopped, the lever falls rapidly for a certain distance, but the muscle does not quite return to its normal length for some few seconds. This residue contraction is easily overcome by any substantial load. If kept in a state of tetanus by weak stimulation, after some time the muscle commences to relax from fatigue, at first rapidly, then more slowly; this falling-off of the tetanic contraction may be prevented by increasing the stimulus.

MUSCLE TONE.

Although the tracing drawn by a lever attached to a muscle in tetanus is straight, and does not show any variation in the tension of the tetanised muscle, some variation in tension must occur, since a low humming sound is produced during contraction. This muscle-tone can be heard by applying the ear firmly over any large muscle (biceps) while in tetanus, or by throwing the muscles attached to the Eustachean tube into action, as in swallowing, or during spasm of the muscles in mastication.

The number of vibrations of the muscle-sound has been estimated to be from 18—20 for the human skeletal muscles. This number of vibrations, however, does not produce any audible note; hence it has been supposed that the note we hear is really the first overtone, and not the fundamental tone. When a muscle is thrown into tetanus by a current interrupted by a tuning fork, a tone is said to be produced which corresponds to the number of vibrations of the fork which causes the interruption in the current, and thus regulates the number of stimulations which the muscle receives. If, however, a contraction of the muscle be brought about by stimulating the spinal cord, with the same apparatus for making and breaking the current, then the normal muscle-tone is produced, just as if the contraction was the result of a nerve impulse coming from the brain.

IRRITABILITY AND FATIGUE.

The life of the muscle tissue of mammalian animals is closely dependent upon a good supply of nutrition, and if its blood current be completely cut off by any means for a length of time it loses its power of contracting. While the muscle remains in the body, and is therefore kept warm and moist by the juices in the tissues, it will live a very considerable time without any blood flowing through it, and it at once regains its contractility when the blood stream is again allowed to flow through its vessels. This is seen when the circulation of a limb is brought to a standstill by means of a tourniquet or a tightly applied bandage. When removed from the body, a mammalian muscle soon ceases to be irritable and dies, but its functional activity may be renewed by passing an artificial stream of arterial blood through its vessels, and an isolated muscle may thus be made to contract repeatedly for a considerable time.

On the other hand, the muscle of a cold-blooded animal will remain alive for a long time—many hours—if kept cool and moist. When its functional activity is about to fade, it may be revived by means of an artificial stream of blood being caused to flow through its vessels, just as in the case of the mammalian muscle.

Common experience teaches us that even when well supplied with blood our own muscles become fatigued after very prolonged exertion, and are incapable of further action. This occurs all the more rapidly when anything interferes with the flow of blood through them, such as when we use our arms in an elevated position; the simple operation of driving in a screw overhead is soon followed by pain and fatigue in the muscles of the forearm, though the same amount of force could be exerted when the arms are in a dependent posture without the least feeling of fatigue.

The difficulties of experimenting with the muscles of mammals make the frog-muscle the common material for investigation, and from it we learn the following facts :—

When removed from the body and deprived of its blood supply, the muscle of a cold-blooded animal slowly dies from want of nutrition. However, if it be placed under favourable circumstances, and allowed perfect rest, it may live twenty-four hours. If it be frequently excited to action, on the other hand, it rapidly loses its irritability, becoming in fact fatigued.

From a muscle removed from a recently killed animal, we learn, moreover that even without any blood supply the muscle-tissue is capable of recovering from very well-marked fatigue, if it be allowed to rest for a little time, so that the muscle has in itself the material requisite for its recuperation.

The first question then is, what causes the loss of irritability which we call fatigue? And the second is, by what means is the muscle *enabled to return to* a state of functional activity? We know that the mere life of a tissue must be accompanied by certain chemical changes which require (1) a supply of fresh material, and (2) the removal of certain substances which are the outcome of the tissue-change. In the case of muscle this chemical interchange is constantly but slowly going on between the contractile substance and the blood. When the muscle contracts much more active, and probably different, changes go on in the contractile substance, more new material being required, and more effete matter being produced. It is probable that the accumulation of these effete matters is the more important cause of the loss of irritability in a muscle, for a frog's muscle when quite fatigued may be rendered active again by washing out its blood vessels with a stream of salt solution of the same density as the serum (·6 per cent. NaCl), and thus removing the injurious "fatigue-stuffs," as they have been called. We know also that a very minute quantity of lactic acid injected into the vessels of a muscle destroys its irritability, and brings it to a state resembling intense fatigue. Of the new material required for the sustentation of muscle irritability we know that oxygen is amongst the most important, though its supply is not absolutely necessary for the recuperation of a partially exhausted, isolated frog's muscle.

The slow recovery of a bloodless muscle from fatigue may be explained by supposing time to be necessary for the reconstruction of new contractile material, and probably also for a secondary change to take place in the effete materials by which they become less injurious.

When working actively, then, it is obvious that the muscles require an adequate supply of good arterial blood in order to ward off exhaustion; and, as already explained in speaking of the vasomotor influences, a muscle does in reality receive a much greater supply of blood when actively contracting than when in the passive state.

The irritability of a muscle and the rate at which it becomes exhausted may be said to depend upon :—

1. The adequacy of its blood supply: the better the supply of new material and the more quickly the injurious effete materials are removed, the more work a muscle can do without becoming exhausted.

2. Temperature has a marked effect on the irritability as well as form of contraction of muscles. Very low temperatures — approaching zero C.—diminish the irritability of a muscle, but do not seem to tend towards more rapid exhaustion. High temperatures —*approaching* 30° C.—increase the irritability, and at the same time *rapidly* bring about fatigue. At about 35° C. an isolated frog's muscle

begins to pass into heat tetanus, and soon loses its irritability for ever.

3. Functional activity is accompanied by an increased blood-supply, and a more perfect nutrition of the muscles, and hence use is advantageous for their growth and power ; while, on the other hand, continued and prolonged inactivity causes a lowering of the nutrition and loss of irritability. Thus when the nerves supplying the voluntary muscles are injured, there is considerable danger of atrophy and tissue-degeneration of the muscles ; the contractile substance becomes replaced by fat granules. This degeneration also occurs in the stump when a limb is amputated, the distal attachments of the muscles having been cut, they atrophy ; for, although their nervous supply is uninjured they cannot act, and after some time muscle tissue can hardly be recognised in them.

DEATH RIGOR.

The death of muscle tissue is preceded by, and associated with, a set of changes which are a kind of exaggeration of those observed in its active state. The most obvious phenomenon is an unyielding contraction, which causes the stiffening of the body after systemic death. Hence it is called *rigor mortis.* The muscles harden ; lose their elasticity, and the tissue is *torn* if forcibly stretched. When isolated, the muscle is seen to be opaque, and its reaction is found to be distinctly acid. A considerable quantity of heat is developed during the progress of the rigor. The electric currents alter in direction and finally disappear.

The period at which rigor comes on, as well as the time it lasts, depend on (*a*) the state of the muscles themselves, and (*b*) the circumstances under which they are placed at the time of death. All influences which tend to facilitate the approach of tissue-death also tend to induce early and rapidly-terminating rigor, viz., (1.) Prolonged activity—as may be shown in a muscle artificially tetanised, or may be seen in an animal whose death was preceded by intense muscular exertion—causes rigor to appear almost immediately, and to terminate rapidly. (2.) Within certain limits, a high temperature facilitates the production of rigor in dying muscles, and indeed a temperature not much exceeding that normal to the tissue induces rigor immediately. This form of contraction, which is called *heat-rigor*, is brought about in mammalian muscles by a temperature of about 50° C., and in frogs' muscles below 40° C. If, however, the temperature of a muscle be suddenly raised to the boiling point, it is killed, and the chief phenomena of rigor are prevented from occurring. (3.) Freezing postpones the appearance of the changes in the muscles upon which rigor depends. (4). Stretching, or any mechanical excitation which tends to injure or hasten the death of the tissue, causes it to pass more rapidly into rigor. (5.) The application of water and of a number of chemical substances causes muscles quickly to pass into a state of rigor similar in all essential respects to that which ordinarily follows the death of the tissue. (6.) Any stoppage in the blood-current normally flowing through a muscle, after some little time makes it pass into a state of rigidity like rigor mortis, but this may be removed by allowing the blood to flow freely again through the muscle.

It is generally admitted that muscle rigor depends on the coagulation of the muscle plasma, giving rise to myosin and muscle serum. This is in most respects comparable with the coagulation of the blood, and also seems to be produced by the action of some ferment, of which several have been made out in dead muscle tissue (compare the par. on chemistry, p. 369).

Most of the phenomena of the process of muscle-rigor remind us of the changes which were noted as occurring in muscle, when it passes from the passive to the active state. Thus the shortening of the fibres, the evolution of heat, and the chemical changes may be said to be identical in contraction and rigor mortis. The electrical changes are, however, very transitory, and are followed by complete loss of elasticity and irritability. Opacity of the tissue accompanies its later stages.

Thus, while dying, the muscle tissue may be said to go through a series of events analogous to those which would occur in a prolonged contraction without any period of recuperation. The idea naturally has suggested itself to the minds of physiologists that the active state of muscle depends upon chemical changes which are the initial steps in the coagulation of the contractile substance, when the muscle is dying. The muscle tissue is supposed to contain a special proteid of extremely intricate and unstable chemical constitution, which, like all plasmata, is constantly undergoing slow molecular change, and which if not re-integrated by constant assimilation would pass into coagulation. Under the influence of stimuli a comparatively sudden and intense molecular disturbance is brought about, which produces shortening of the fibres and the same chemical changes as precede the coagulation. Before the stage of coagulation appears, however, a chemical re-arrangement takes place, the result of which is the re-construction of the unstable complex proteid. If nutriment be withheld, or if the stimulation be too powerful, the recovery cannot take place, and we find the muscle passing from a state of physiological contraction to one of intense exhaustion, and then to coagulation and death.

UNSTRIATED MUSCLE.

So far reference has only been made to the skeletal muscles, the fibres of which are marked by transverse striations, and whose single contraction is extremely rapid and short. The contractile tissues which carry on the movements in the various organs of the body are not striated fibres, but, as has been already stated, consist of elongated flattened cells with rod-shaped nuclei. They occur generally in the form of sheets or layers forming coats for the organs in which they lie. Their single contraction is slow and prolonged, and commonly is transmitted from one muscle-cell to another as a kind of sluggish wave. They are incapable of passing into a tetanic state of contraction like striated muscles.

The slowest contraction seems to be that of the little muscle-cells in the walls of the blood-vessels. These remain in a state of partial contraction, which undergoes a brief and partial rhythmical relaxation. The most forcible aggregate of unstriated muscle elements is met with in the uterus. This organ, which has very exceptional motor powers to perform, contracts in somewhat the same way as the muscles of the blood-vessels, but more quickly, and with longer rhythmical intervals of partial relaxation. The muscular wall of the intestine and the iris are among the most rapidly contracting smooth muscles.

The chemical properties of the smooth muscle are much the same as those of striated skeletal muscles, and they pass into a state of rigor, while dying, which seems to depend on the same causes as the rigor mortis already described.

CHAPTER XXVI.

THE APPLICATION OF SKELETAL MUSCLES.

The consideration of the many varieties of muscles, and the various modes in which they are attached to the bones that they are destined to move, belongs to the department of practical anatomy, and needs no mention here. As a general, but by no means universal rule, a muscle has one attachment which is fixed, commonly spoken of as its *origin*, and a second, called its *insertion*, upon which it acts by approximating it to the origin. Muscles mostly pass in a straight line between their two attachments, but sometimes they act round an angle by sliding over a pulley, or by means of a small bone in the tendon, like the patella.

The muscles are so attached that they are always slightly on the stretch, and thus at the moment they begin to contract they are in an advantageous position to bring their action to bear on the bones which they move. When the contraction ceases the bones are drawn back to their former position without any sudden jerk or jar.

The muscles commonly act upon the bones as levers by working upon the short arm of the lever, so that more direct force is required on the part of a muscle than the weight of the body moved; but from this arrangement considerable advantages are gained, viz., that a small contraction of the muscle causes an extensive excursion of the part moved, and much greater rapidity of motion is attained.

All the three orders of levers are met with in the movements of the different bones of the skeleton; often, indeed, all three varieties are found in the same joint, as the elbow, where the simple extension and flexion motions of the biceps and triceps muscles give us good examples (Fig. 194).

The first order of lever is used when the triceps is the power and draws upon the olecranon, thus moving the hand and forearm around the trochlea which acts as the fulcrum. This is shown in the upper diagram, in which the hand is striking a blow with a dagger.

The second order comes into play when the hand, resting on a point of support, acts as the fulcrum, and the triceps pulling on the olecranon is the power which raises the humerus upon which is fixed the body or weight (middle diagram).

The third order may be exemplified by the action of the biceps in ordinary flexion of the elbow. Here the muscle, which is the power, is placed between the fulcrum—represented by the lower end of the humerus—and the weight which is carried by the hand (lower diagram).

The various groups of muscles which are so arranged as to assist each other when acting together, are called *synergetic,* and those which when contracting at the same time oppose each other, are called *antagonistic.* The same muscles may, in different positions of a joint or in combination with other different muscles, have totally different actions, at one time being synergetic and at another antagonistic. Thus, the sterno-mastoid muscle may, in different positions of the head, either bend the cranium backwards or forwards, and so co-operate with two sets of muscles which are definitely antagonistic to one another.

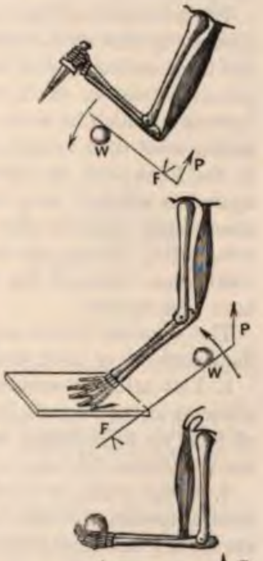


Fig. 194.—Diagrams showing the mode of action of the three orders of levers (numbered from above downwards) illustrated by the action of the elbow joint.

JOINTS.

The unions between the bones of the skeleton are very varied in function and character. They may be classified as :—

1. SUTURES, in which the bones are firmly united by rugged surfaces without the interposition of any cartilage. They are practically only the lines of union of different bones, which grow together to form a single bone.

2. SYMPHYSES, in which two bony substances are strongly cemented together by ligaments, and a more or less thick adherent layer of fibro-cartilage, are joints allowing of some movement, which is, however, very *limited.*

3. DIARTHROSIS, or true movable joints, such as are commonly met with in the extremities. They are characterised by a synovial sac lining the surrounding ligaments, and two smooth surfaces of cartilage which cover over the bony extremities taking part in the articulation, and form what are called the articular surfaces. The synovial sac is strengthened by a loose membranous covering—the capsular ligament—which is attached round the edge of the cartilages next to the periosteum, which here ceases.

The articular surfaces are always in exact and close contact, being pressed together by the following influences:—(1.) The elastic tension and tonic contraction of the surrounding muscles, which exert considerable traction on them. (2.) The traction of the surrounding ligaments, which in some cases holds the bones firmly together, no matter what their relative positions may be. This can be well seen in the knee-joint, in which a comparatively small number of the ligaments suffice to keep the articular surfaces in contact. (3.) The atmospheric pressure also tends to hold the bones in close apposition, as may be seen in the hip-joint, which is not easily disarticulated, even when all the surrounding structures and the ligaments have been severed.

The synovial joints may be classified according to the form of their surfaces, or their mode of motion, as follows:—

1. Flat articular surfaces held together by a short rigid capsule allowing of but very slight gliding movement; examples of this form of joint are to be found in the tarsus and the articular processes of the vertebræ.

2. Hinge joints, in which the surfaces are so adapted that only one kind of motion can take place. A groove-like cavity in one bone fits closely and glides around the axis of a roller on the other bone, while the sides of the joint are kept tightly together by means of strong lateral ligaments. Examples of this form of joint are to be found between the phalanges of the digits and at the humero-ulnar joint.

3. The rotatory hinge, or pivot joint, is that in which a part moves round the axis of a bone, instead of the axis of rotation being at right angles to both bones forming the joint as in an ordinary hinge. Such joints are seen at the head of the radius and in the articulation between the atlas and the odontoid process of the axis.

4. A saddle-shaped joint is a kind of double hinge, in which each of the two articulating bones form a partial socket and roller, and [illegible] rotation placed more or less at right

angles one to the other. A good example of this kind of joint occurs between the thumb and one of the wrist bones.

5. Spiral articulations are modifications of the hinge, in which the surface of the roller does not run "true," but becomes eccentric, so that the surface of the roller forms really a part of a spiral by means of which the bone articulating with it is forced away from the central axis of rotation and becomes jammed as if stopped by a wedge. The best example of this is the knee. In this joint the axis of rotation is near the posterior surfaces of the bones, and passes transversely through the condyles of the femur, the surfaces of which form an arc, the centre for which corresponds to the axis of motion. In ordinary flexion the head of the tibia moves on the arc around the axis so as to partially relax the lateral ligament and allow of some rotation on the axis of the tibia. When the head of the tibia moves forwards, in extension, it becomes wedged against the anterior part of the articular surface of the femur, which presents an eccentric spiral-like curve, departing more and more from the centre of rotation as the articular surface of the tibia proceeds forwards. The effect of this is, that in extension of the leg the ligaments are made tense, and the bones are firmly locked together. Owing to the inequality between the size of the internal and external condyles the axis of rotation is not at right angles to the axis of the femur, but is at such an angle that extreme extension causes also a slight amount of outward motion of the leg.

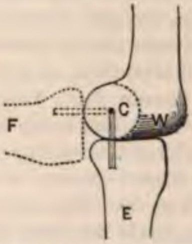


Fig. 195.—Diagram of the action of the knee-joint.

W = articular surface of femur.
E = tibia in position of extension.
F = tibia in position of flexion.
C = centre of rotation.

6. In the ball and socket joints—the name of which implies their mechanism—the most varied movements occur. (Hip and shoulder.)

STANDING.

In order that an elongated rigid body may stand upright it is only necessary that a line drawn vertically through its centre of gravity should pass within its basis of support, and if the latter be sufficiently wide the object will remain permanently in that position. The human body is, however, in the first place not rigid, and in the second place the basis of support is too small to ensure a satisfactory degree of steadiness. The act of standing must, therefore, be accomplished by the action of certain muscles, which are employed in preventing the different joints from collapsing, and in so balancing the various parts of the body as to keep the whole frame from toppling over.

In order to economise muscular energy while standing, we must lock as many of our joints as possible, and thus depend rather on the passive ligaments than upon muscle action for the rigidity of the body. With this object we are taught to place the heels together, turn out the toes, bring the legs parallel by approximating them, and extending the knees to the utmost, to straighten and to throw back the trunk so as to render tense the anterior hip ligaments, to direct the face straight forwards so as to balance the head evenly, and to let the arms fall by the sides.

In this position, as a soldier stands at attention, the knee and hip joints remain fixed, without any effort on the part of the muscles, but it is far from being the most comfortable attitude one can assume for prolonged standing, and hence the position known best by the order "stand at ease" is adopted if more complete rest is desired. In this position the weight of the body is usually allowed to rest on one leg while the other lightly touches the ground to form a kind of stay and relieve the muscles which surround the supporting ankle from too great an effort of balancing. At the same time the knee is extended and the pelvis becomes somewhat oblique so as to bring it more directly over the head of the femur. In ordinary easy standing, the joints are not commonly kept locked by the tension of the ligamentous structures, but their position is constantly being very slightly altered so as to vary the muscles employed in preserving the balance and thus to prevent fatigue.

The joints most exercised in the erect posture are the following :—

1. The *ankle* has to support the weight of the entire body, while the joint is neither flexed nor extended to its utmost, and cannot be fixed in this position by ligamentous arrangements. The foot being placed on the ground, resting on the heel and the balls of the great and little toes, is supported in an arch-like form by strong, though elastic, ligaments, which allow but little motion in the numerous joints. The bones of the leg can move in the freest way, backwards or forwards, around the articular surface of the astragalus, which forms the roller of the hinge, any lateral motion of which is prevented by the malleoli. The line passing through the centre of gravity of the body generally falls slightly in front of the axis of rotation of the ankle-joint, so that the entire body tends to fall forwards at the

ankles. This tendency is checked by the powerful calf muscles, which, attached to the calcaneum by means of the strong tendo Achillis, keep the parts in such a position that an exact balance is nearly constantly kept up.

2. The *knee-joint*, when completely extended, requires no muscular action to prevent it from bending, because the line of gravity then passes in front of the axis of rotation, and the weight of the body tends to bend the knee backwards. This is impossible on account of the powerful ligaments which exert their traction behind the axis of rotation. Commonly, however, these ligaments are not put on the stretch in this way, but the joint is held, by muscular power, in such a position that the line of gravity passes just through, or very slightly behind, the axis of rotation of the joint, so that, if anything, there is a slight tendency for the knee to bend. This is completely checked, and the body balanced by the powerful extensor muscles of the thigh.

3. In the *hip joints*, which have to support the trunk and head, the line of gravity falls just behind the line uniting the joints when the person is perfectly erect, so that here the body has a tendency to fall backwards. This is prevented by the strong ilio-femoral ligament. When, however, the knee is not straightened to the full extent, so that the line of gravity passes through or a little behind the axis of rotation of that joint, then the pelvis is very slightly flexed on the femora so that the axis of the joints lies exactly in or a little behind the line of gravity, and thus the body inclines rather to fall forwards. This tendency, however, is prevented by the powerful glutei muscles, which also enable us to regain the erect posture after bending the trunk forwards.

The motions of which the *pelvis* and *vertebral column* are capable are too slight to deserve attention here. The vertebral column, wedged in as it is between the two innominate bones, may be taken, together with the pelvis, as forming a very yielding and elastic, but practically jointless, pillar, the upper part of which can alone be bent to such an extent as to require mention in discussing the mechanism of station.

The individual joints between *the cervical vertebræ* permit but a slight amount of movement when taken separately, but by their aggregate motion they enable considerable extension and flexion of the neck to take place. These motions follow so closely, and are so inseparably associated with those of the head on the upper vertebra, that there is no need to consider them separately from the latter.

The *atlanto-occipital joints* admit of some little lateral movement, but that in the antero-posterior direction is much the more important, but even this would be insignificant were it not associated with the movements between the other cervical vertebræ.

The cranium has then to be balanced on the top of a flexible column, and rests immediately in a kind of socket, which can move as a double hinge around two axes at right angles one to the other. The vertical line from the centre of gravity of the cranium must vary with every forward, backward, or lateral movement of the head or neck, but in the erect posture it passes a little in front of the axis of rotation of the atlanto-occipital joint and somewhat behind the curve of the cervical vertebræ, so that the head may be said to be poised on the apex of the vertebral column, with some tendency to fall forwards. There are no ligamentous structures which can lock the joints so as to keep the head in the erect position; therefore without the aid of muscular force the head will fall forwards or backwards according to the position it is in when the muscles become relaxed as in sleep.

From the foregoing facts it will be seen that there exists a kind of co-ordinated antagonism at work in ordinary easy standing which keeps the elastic pliable body upright, without the rigidity adopted when standing "at attention." The muscular action is more exercised when we are not on steady ground and varied co-ordination becomes necessary; for instance, when we go on board ship for the first time. Station then takes some little time to become perfected, and requires new associations of movement. The gastrocnemius and soleus relax the ankle in a degree just proportionate to the amount of flexion of the knee permitted by the quadriceps extensor cruris, while simultaneously the great gluteal muscle allows the body to incline forwards so as to keep its centre of gravity in the proper relation to the basis of support.

WALKING AND RUNNING.

The common act of progression is accomplished by poising the weight of the body alternately on one leg—called the supporting limb—and, with the other—the pendulous limb—tilting the body forwards out of equilibrium, and then swinging the latter limb forwards and placing it in front so as to prevent the body falling forwards. In its turn this then becomes the supporting leg. The swinging leg is described as having two phases, (1) active while pushing off from the ground, and (2) passive, while swinging forwards like a pendulum. In starting, one foot is placed behind the other, so that the line of gravity lies between the two, the hindmost limb having the ankle and knee a little bent. By suddenly straightening these joints it gives a "push off" with the toes and propels the body forward so as to move it around the axis of motion of the fixed or supporting ankle-joint. At the end of the swing, the pendulous leg comes to the ground and leaves the other limb in the attitude ready for the push off. Thus on level ground walking is carried on with but small muscular exercise; but in ascending a steep incline or going up stairs, the supporting limb has to elevate the body at each step by extending the knee and ankle joints by the thigh extensors and the calf muscles.

Running is distinguished from walking by the fact that, while in the latter both feet rest on the ground for the greater part of each pace, in the former the time that either foot rests on the ground is reduced to a minimum, and in fact the supporting limb disappears. The legs are kept in a semi-flexed position ready for the push off or spring, which is so forcibly carried out that the body is propelled through the air without any support. Thus an interval—of greater or less duration according to the pace—exists during which both the feet are off the ground, as the moment either foot comes to the ground it executes a new spring without waiting for the pendulous swing described in walking.

CHAPTER XXVII.

VOICE AND SPEECH.

THE human voice is produced by an expiratory blast of air being forced through the narrow opening at the top of the windpipe called the glottis. This glottis, which lies in the lower part of the larynx, is bounded on each side by the edges of thin, elastic, membranous folds that project into the air-passages. These membranous folds, called the vocal cords, are set vibrating by the current of air from below, and in turn communicate their vibrations as sound to the air in the air-passages situated above them.

ANATOMICAL SKETCH.

The vocal apparatus is really a musical instrument of the reed-pipe kind. If we compare it with the pipe of an organ, we find all the parts of the latter represented. The lungs within the moving thorax act as the bellows. The bronchi and trachea are the supply pipes and air box. The vocal cords are the vibrating tongues ; while the larynx, pharynx, mouth, and nose, act as the accessory or resonating pipes. The blast of air is produced and regulated by the respiratory muscles; and special intrinsic muscles of the larynx change the conditions of the vocal cords so as to alter the pitch of the notes produced. Other sets of muscles, by altering the conditions of the resonating pipes, give rise to many modifications in the vocal tones, and thus produce what is called *speech*.

The larynx, which may be regarded as the special organ of voice, is, in the main, made up of four cartilages, viz., the cricoid, thyroid, and two arytenoids, jointed together so as to allow of considerable motion. Of these the inferior, the cricoid, is attached to the trachea which it joins to the others. It forms a ring, which is thin in front, but deep and thick behind, owing to a peculiar projection upwards of its posterior part. The thyroid consists of two side wings so bent so as form the greater part of the anterior and lateral boundaries of the voice box, and can be felt easily in the front of the throat. It is articulated to the sides of the cricoid by its two inferior and posterior extremities, so that the upper part of the cricoid cartilage can move backwards and forwards. The arytenoid cartilages are little three-sided pyramidal masses placed on the upper surface of the posterior part of the cricoid, to which they are attached by a loose joint. They are so placed that one surface looks inwards, the second backwards, and the third forwards and outwards, while the inferior surface rides on the cricoid. One point, therefore, looks forwards, and to it is attached the vocal cord on each side, hence it has been called the vocal process. The apex, which looks outwards and backwards, gives attachment to some of the intrinsic muscles and hence has been called the muscular process.

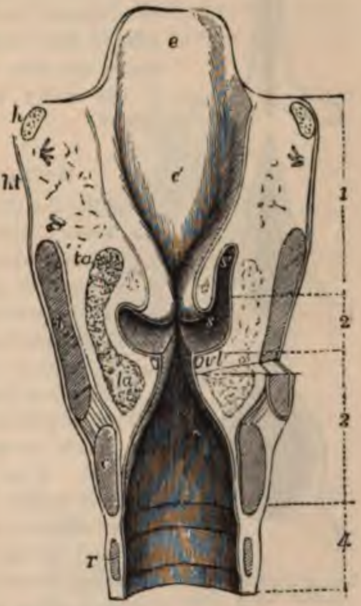


Fig. 196.—Anterior half of a transverse section through the larynx near its middle. More is cut away on the upper part of the right side. 1. Upper division of the laryngeal cavity; 2. Central portion; 3. Lower portion continued into 4, trachea; *e*, epiglottis; *e'*, its cushion; *t*, thyroid cartilage seen in section. *vl*, true vocal cord at the rima glottidis; *s*, ventricle of larynx; *s'*, saccule. (A. Thomson.)

The thyroid cartilage is connected with the cricoid below, and to the hyoid bone above by ligaments and tough membranes, which hold the parts together, fill in the intervals, and complete the skeleton of the larynx.

The vocal cords are composed of small strands of elastic tissue, which are stretched between the anterior processes of the arytenoid cartilages and the inferior part of the thyroid, where they are attached side by side to the posterior surface of the angle formed by the junction of *the two lateral* parts or alæ of the thyroid. The mucous membrane which lines the larynx is thin, and closely adherent over the vocal cords. The surface of the laryngeal cavity is smooth and even, the lining membrane passing over the cartilages and muscles so as to obliterate all ridges except the vocal cords and two others, less sharply defined, called the false vocal cords, which lie parallel to and above the true vibrating cords. Between these is the cavity known as the ventricle of the larynx.

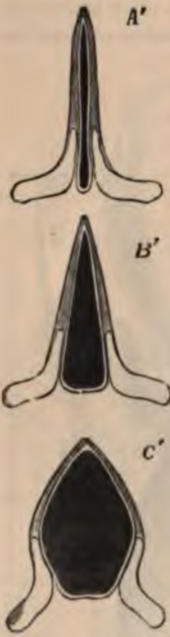


Fig. 197.—Three diagrams taken from laryngoscopic views of the superior aperture of the larynx showing the position of the vocal cords and the arytenoid cartilages supposed to be seen in transverse section during different actions of the larynx.

A'. Vocal chink as in singing.
B'. In easy quiet inhalation of air.
C'. In forced inspiration.

Mechanism of Vocalisation.

Taking the thyroid cartilage as the fixed base, the cricoid and arytenoid cartilages undergo movements which bring about two distinct sets of changes in the glottis and its elastic edges, namely, (1) widening and narrowing the opening; (2) stretching and relaxing of the vocal cords. During ordinary respiration the glottis remains about half open, the muscles being in a state of relaxation (B'). During forced inspiration the glottis is widely dilated by muscular action (C'). If an irritating gas be inspired, the glottis is tightly closed by a spasmodic action of certain muscles, so that the true vocal cords act as a kind of valve.

During vocalisation the glottis is formed into a narrow chink with parallel sides (A'), while the cords are made more or less tense, according to the pitch of the note to be produced; both these changes being brought about by muscular action.

The opening of the chink of the glottis is accomplished chiefly by a muscle called the posterior crico-arytenoid, which passes from the posterior surface of the cricoid cartilage to the outer and posterior angle of the arytenoids. By pulling the latter point downwards and backwards it separates the arytenoid cartilages, particularly at their anterior extremity, where the cords are attached. In this action they are aided by a small muscle connecting the posterior surfaces of the arytenoid, namely, the posterior arytenoid, which tends, when the two arytenoid cartilages are held apart, to rotate them so that the vocal processes are separated.

The narrowing of the glottis is executed by the lateral crico-arytenoids which run upwards and backwards from the antero-lateral aspect of the cricoid to the muscular processes of the arytenoid cartilages. They pull the muscular processes forwards, and thus rotate the arytenoid cartilages so as to approximate the vocal processes to one another, while any tendency towards pulling apart the bodies of the cartilages, owing to the downward direction of the muscle, is overcome by the posterior arytenoid muscle and those muscular bands which pass from the posterior surface of the arytenoid cartilages to the epiglottis and the upper part of the thyroid cartilage, the external thyro-arytenoid, and the thyro-ary-epiglottic muscles (Henle). The other fibres, which pass directly from the arytenoid to the thyroid cartilages—internal and external thyro-arytenoid muscles—in the same direction as the vocal cords, complete the closure by helping to press together the

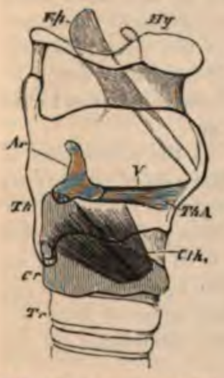


Fig. 198.—Diagram of the side view of the larynx showing the position of the vocal cords (v). (Huxley.)

Ar. Arytenoid cartilage.
Hy. Hyoid bone.
Th. Thyroid cartilage.
Cr. Cricoid cartilage.
Tr. Trachea.
C.th. Crico-thyroid muscle.
Th.A. Thyro - arytenoid muscle.
Ep. Epiglottis.

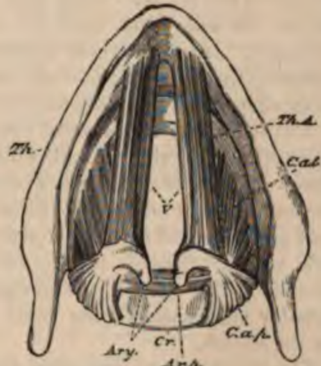


Fig. 199.—Diagram of the opening of the larynx from above. (Huxley.)

Th. Thyroid cartilage.
Cr. Cricoid cartilage.
Ary. Superior extremities of the arytenoid cartilages.
V. Vocal cords.
Th.A. Thyro-arytenoid muscles.
C.a.l. Lateral crico-arytenoid muscle.
C.a.p. Posterior crico-arytenoid muscle.
Ar.p. Posterior arytenoid muscle.

vocal processes and by approximating the cords themselves. In spasmodic closure of the glottis, all these latter muscles act violently together, and have been grouped by Henle as the constrictor of the glottis. Relaxation of the vocal cords accompanies voluntary closure of the glottis, as in holding the breath, when the false vocal cords are said to have a valvular action. But the muscular fibres, which run from the arytenoid cartilages to the thyroid, nearly parallel to the true vocal cords, are those concerned in the act of relaxation when the cords are active. They pull forwards the arytenoid cartilages, and at the same time draw the upper part of the cricoid slightly forwards. Moreover, these muscles have an all-important action in adapting the edges of the cords and the neighbouring surfaces to the exact shape most advantageous to their vibration.

The stretching of the vocal cords is caused by the contraction of one muscle, the crico-thyroid, which, on the outer side of the larynx, passes downwards and forwards from the lower part of the thyroid to the anterior part of the cricoid cartilage. It thus pulls the anterior part of the cricoid cartilage upwards, causing it to rotate round an axis passing through its thyroid joints. The upper part of the cricoid, which carries the arytenoids, is thus removed from the anterior attachment of the vocal cords, and the membranes are put on the stretch.

The requirements necessary for the production of voice are the following :—

1. Perfect elasticity and clearness of edge of the vocal cords, and freedom from all surface irregularity, such as would be caused by thick mucus adhering to them, or any abnormality.

2. The cords must be very accurately adjusted, closely approximated together, and kept parallel, almost touching each other evenly throughout their entire length.

3. The cords must be held in a certain degree of tension, or the vibration does not produce any vocal tone, but simply a raucous noise.

4. The air must be propelled through the glottis by a *forced expiration.* The normal expiratory current is too gentle to give the necessary vibration. After the operation of tracheotomy, the air escapes through the abnormal opening, and sufficient pressure cannot be brought to bear on the cords, so no vocal sound can be produced, and the person speaks in a whisper, unless the exit of air through the tracheotomy tube is prevented by placing the finger temporarily upon the opening.

PROPERTIES OF THE HUMAN VOICE.

In the voice we can recognise the same properties as are noted in other kinds of sound. These are quality, pitch and intensity.

(1.) The *quality* of vocal sounds is almost endless in variety, as is shown by the vocal capabilities of different individuals. The quality of tone of any musical sound depends upon the relative power of the fundamental note, and of the overtones that accompany it. The less disturbed the fundamental notes are by overtones, the clearer and better is the voice. This difference in quality of the human voice depends upon the perfectness of the elasticity, the relation of thickness to length, surface smoothness, and other physical conditions of the cords themselves, and the exactitude with which the muscles can adapt the surfaces. For singing well, much more is necessary than good quality of tone, which is common enough. The muscles of the larynx, thorax, and mouth must be all educated to an extraordinarily high degree.

(2.) The *pitch* of the notes produced in the larynx depends upon—first, the absolute length of the vocal cords. This varies with age, particularly in males, whose vocal organs undergo rapid growth at puberty, when the voice is said to *crack*. The vocal cords of women have been found by measurement to be about one-third shorter than those of men, and people with tenor voices have shorter cords than basses or baritones. Secondly, on the tension of the cords: the tighter the vocal cords are drawn by the crico-thyroid muscles, the higher the notes produced; and the well-known singer Garcia believed he observed with the laryngoscope the vocal processes so tightly pressed together as to impede the vibration of the posterior part of the cords, and by this means they could be voluntarily shortened.

(3.) *Intensity* or loudness of the voice depends solely on the strength of the current of air. The more powerful the air-blast the greater amplitude of the vibrations, and hence the greater the sound produced. The narrower the chink of the glottis, and the tighter the parallel cords are stretched, the less is the amount of air and the weaker is the blast required to set them vibrating; and *vice versâ*, the looser the cords and the wider apart they are, the greater the volume and the force of the air current necessary for their complete vibration. Hence it is that an intense vibration or loud note can be produced much more easily with notes of a high pitch than with very low notes, and we find singers choosing for their telling *crescendo* some note high up in the range of their voice.

The human voice, including all kinds of voice, extends over about three and a-half octaves. Of this wide range a single individual can seldom sing more than two octaves. The soprano, alto, tenor, and bass forming a descending series, the range of each one of which considerably overlaps the next in the scale.

During the ordinary vocal sounds, the air, both in the resonating tubes above the larynx and in the windpipes coming from below, is set vibrating, so that the trachea and bronchi act as resonators as well as the pharynx, mouth, &c. This may be recognised by placing the hand on the thorax, when a distinct vibration is communicated from the chest wall. Such tones are, therefore, spoken of as chest notes. Besides the chest tones of the ordinary voice, we can produce notes of a higher pitch and a different quality, which are called head notes, since their production is not accompanied by any vibration of the chest wall. The physical contrivance by means of which this *falsetto* voice is brought about is not very clearly made out. The following are the more probable views:—(1) It has been suggested that in falsetto only the thin edges of the cords vibrate, the internal thyro-arytenoid muscles keeping the base of the cord fixed; while with chest tones a greater surface of the cord is brought into play. (2) The cords are said to be wider apart in falsetto than in chest notes, and hence the trachea, &c., ceases to act as a resonator. (3) Or the cords may be arranged so that only one part of them, the anterior, can vibrate, and thus they act as shortened cords, a "stop" being placed on the point where the vibrations cease, by the internal thyro-arytenoid muscle.

The production of a falsetto voice is distinctly voluntary, and is probably dependent upon some muscular action in immediate relation to the cords, for it is always associated with a sensation of muscular exertion in the larynx as well as with changes that take place in the conformation of the mouth and other resonating tubes.

NERVOUS MECHANISM OF VOICE.

The nervous mechanism by means of which vocal sounds are produced is among the most complexly co-ordinated actions that regulate muscular movements.

Like respiration, vocalisation at first seems a simple voluntary act, sounds of various kinds being produced at the command of the will of the individual. No doubt the respiratory muscles, which work the bellows of the voice organ, are under the control of the will so long as the respiration is not interfered with. The mouth and throat muscles which shape the resonating tube are also voluntary. But the intrinsic muscles of the larynx are only voluntary in a certain sense, while in another they are distinctly involuntary, as may be seen in spasm of the larynx; for they are, in part at least, controlled by impulses which arise at the organ of hearing and pass to some co-ordinating centre, which arranges the finer muscular movements necessary to produce a certain note. When we sing any note struck on a musical instrument, we set the expiratory, mouth, and general vocalising muscles in readiness for the proper application of the air blast by a voluntary act; but the exact tuning of the vocal cords is accomplished in some measure reflexly by impulses coming from the ear to a special co-ordinating centre, the education of which is commonly in advance of the volition centres, and therefore can only be controlled by the latter in persons specially educated to music. Some persons who can sing a given note with promptness and exactitude without any effort, would find much difficulty in overcoming, by volition, the accuracy of this perfect reflex mechanism. In fact, a person with a good ear finds it difficult to sing out of tune, even if he try.

Though we feel that we have command over the pitch of our sound-producing organ, we owe much to the aid of our sound-appreciating organs and the nerve centres which they have in connection with them.

SPEECH.

The variations in vocal sounds which give rise to speech are not produced in the larynx, but in the throat, mouth, and nose. When unaccompanied by any vocal sound, speech only gives rise to a *whisper*; but when a vocal tone is at the same time produced, we have the ordinary loud speaking. Since vocal tones can only be produced by expiration, so we can only speak aloud by means of an expiratory current of air; but an inspiratory current may be made to give rise to a kind of whisper.

Speech is composed of two kinds of sounds, in one of which the sounds must be accompanied by a vocal tone, and are hence called "vowels;" in the other no vocal tone is necessary, but changes in shape take place in the resonating chambers, so as to give rise to noises called consonants. As the pronunciation of the consonants is usually accompanied by some vowel sound, and further from the fact that the difference between the vowels is brought about by changes in the shape of the mouth, the distinction between the two sets of sounds is *rather artificial* than real.

The production of the different vowel sounds depends upon such a change being brought about in the shape of the mouth cavity and aperture, that a resonator with a different individual note is formed for each particular vowel.

The sounds called consonants are caused by some check or impediment being placed in the course of the blast of air issuing from the air-passages. They may be classified, according to the part at which the obstruction occurs, as follows :—

1. *Labials*, when the narrowing takes place at the lips, as in pronouncing *b*, *p*, *f*, *v*.

2. *Dentals*, when the tongue causes the obstruction by being pushed against the hard palate or the teeth, as in *t*, *d*, *s*, *l*.

3. *Gutturals*, when the posterior part of the tongue moves towards the soft palate or pharynx, as in saying *k*, *g*, *gh*, *ch*, *r*.

Consonants may also be divided into different groups, according to the kind of movements which give rise to them.

1. *Explosives* are produced by the sudden removal of the obstruction, as with *p*, *d*, *k*.

2. *Aspirates* are continuous sounds caused by the passage of a current of air through a narrow opening, which may be at the lips, as in *f*, at the teeth as with *s*, or at the throat as in *ch*.

3. *Resonants* are the sounds which require some resonance of the vocal cords, and the air current is suddenly checked by closure of the lips, as in *m*, or the dental aperture as in *n* or *ng*.

4. *Vibratory*, of which *r* is the example, requires a peculiar vibration of the vocal cords, while either the dental or the guttural aperture is partially closed.

CHAPTER XXVIII.

GENERAL PHYSIOLOGY OF THE NERVOUS SYSTEM.

Anatomical Sketch.

The nervous system is the apparatus by which the distant parts of the body are kept in constant relationship with one another, so that a change of state of any one organ is communicated to and may set up corresponding changes in remote parts of the system. It is made up of two varieties of tissue, both of which possess special vital properties. The one, which is composed of thread-like strands of protoplasm—*nerve fibres*—connect together the elements of the other group, the *nerve corpuscles*, which form either peripheral or central terminals. *Nerve fibres* are then simply special conducting agents, having at one extremity a special terminal or nerve cell for sending impulses, and at the other extremity other cells for receiving the same. These terminal organs, between which the nerve fibres pass, are the agents which determine the direction the impulse is to travel along the nerve. The sending organ is some times at the peripheral end of the nerve, and the receiver in the nerve centres, as in the case of an ordinary cutaneous nerve, which carries impulses from the skin to the brain; or these duties of the terminal organs may be reversed, as in the case of the nerves conveying impulses from the brain to the muscles.

The former kind of nerves are called *afferent* or *centripetal*, and the latter *efferent* or *centrifugal*. Nerves are capable of carrying impulses in either direction, as has been proved by cutting the afferent lingual and the efferent hypoglossal nerves and causing the proximal end of the former to unite with the distal end of the latter, which is distributed to the muscles of the tongue. When the union has taken place, a stimulus applied on the afferent portion causes the muscles to move.

Any piece of protoplasm can conduct impulses, as is seen in the rapid transmission of an impulse in animals and textures which have no special conducting elements or nerve fibres. Thus in the hydra all the cells act as nerves, and in the higher animals an impulse, producing a wave of contraction, can pass on from one muscle cell to the other directly, as is seen in the ureter, or in the frog's heart. The only essential part of a nervous conductor is a delicate protoplasmic fibril. Single, thin, thread-like fibrils are commonly found carrying impulses in the nerve centres. But in the nerves distributed about the body one does not meet these single protoplasmic threads (except where the fibrils are interwoven to form terminal networks, as seen in the cornea), but the fibrils are clustered together in large bundles, so as to make one nerve fibre. This bundle of protoplasmic fibrils is, in the peripheral nerves, always covered, and is called the *axis cylinder* of the nerve fibre. In some nerve fibres there is but one very thin transparent covering, termed the *primitive sheath*, while in others there is a thick layer of doubly-refracting fluid inside the primitive sheath, in immediate contact with the fibrils of the axis cylinder. This is called the *medullary sheath*, or white substance of Schwann, because its peculiar refractive properties make it look white when viewed in a direct light. According as the nerves have or have not this medullary sheath, they have been

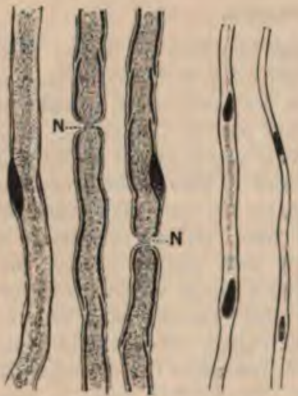


Fig. 200.—Highly magnified view of three medullated and two non-medullated nerve fibres of frog, stained with osmic acid, which makes the medullary sheath black.

N.—Nodes of Ranvier—where the axis cylinder can be seen to pass the gap in the medullary sheath.

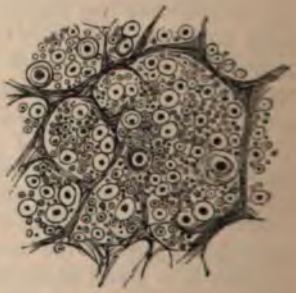


Fig. 201.—Transverse section of nerve fibres, showing the axis cylinders cut across, and looking like dots surrounded by a clear zone, which is the medullary sheath. Fine connective tissue separates the fibres into bundles.

termed "white" or "grey." The former are by far the most plentiful, since they make up the greater part of the ordinary nerves, while the grey fibres only predominate in the sympathetic nerve and its ramifications and parts of the special sense organs.

An ordinary nerve, then, is made up of a large number of fibres, held together by connective tissue, and each of the fibres contains a vast number of fibrils within its sheath.

FUNCTIONAL CLASSIFICATION.

Nerve fibres may be classified according to their function, in the following way:—

I. *Afferent nerves*, those which bear impulses from the surface to the nervous centres. These may be further divided into:

(*a.*) *Sensory nerves*, when the impulse they convey gives rise to a "perception." The perceptions may be the special sensations which are transmitted from the organs of special sense, or those of general sensation, giving rise to pleasure or pain.

(*b.*) *Reflex nerves*, which communicate the impulse to some other nerve elements, and thus give rise to some new forces, without any perception of the stimulus. According to the result of the excitation resulting from their reflected impulse they are termed—excito-motor, excito-secretory, and excito-inhibitory, &c.

(*c.*) Those nerves which act both as sensory and reflex nerves; these are the most numerous, the sensory or reflex action depending upon the condition of the nerve centres.

II. *Efferent nerves*, which carry impulses from the centres to the various organs throughout the body. According to the effect their excitation produces they are termed: (*a*) *motor*, going to muscles and causing them to contract; (β) *secretory*, the stimulation of which calls forth the activity of a gland; (γ) *inhibitory*, when they check or prevent some activity by the impulses which they carry; (δ) *vaso-motor nerves*, which regulate the contraction of the muscular coat of the blood-vessels; (ε) *trophic*, *thermic*, *electric* nerves are also to be named, the two former being of doubtful existence, and the latter being only found in those animals which are capable of emitting electric discharges, such as the electric fishes.

III. *Intercentral nerves* are those which act as bonds of union between the several ganglion cells of the nervous centres, which are connected, in the most elaborate manner, one with the other. As the terminals of these fibres are both probably receiving and directing agents, the delicate strands of protoplasm communicating between them probably convey impulses in different directions, but of this we can have no definite idea, although such a supposition would aid us in forming a mental picture of the manner in which the wonderfully complete intercentral communications are accomplished.

MODE OF INVESTIGATION.

In order to investigate the functions of the different nerves a knowledge of their central connections and their peripheral distribution is necessary. But anatomical knowledge, however perfect, does not convey an adequate notion of their function, as may be amply seen from deductions made by anatomists, many of which have not borne experimental tests.

The procedure adopted in testing the function of a nerve is the following. The nerve is exposed and cut, and it is observed whether there be any loss of sensation or muscular paralysis in the part to which it passes. The cut ends are then stimulated, and the results are observed. The end of the part connected with the centres is spoken of as the central or proximal end, and that belonging to the part leading to the distribution of the nerve, is called the peripheral or distal end. If the nerve be purely motor, stimulation of the proximal end will yield no result, but when the distal end be irritated, active movements follow. If, on the other hand, it be a sensory nerve, stimulation of the distal end gives no result, and that of the proximal end produces signs of pain. In a compound nerve some response is obtained when either the distal or proximal end is irritated.

CHEMISTRY OF NERVE FIBRES.

The axis cylinder of nerves is probably composed, as already mentioned, of protoplasm; further than that nothing is known of its chemical properties. The medullary sheath yields certain substances which are related to the fats, and can be extracted with ether and chloroform. Among these is the peculiar compound nitrogenous fat, lecithin containing phosphorus, also cholesterin, cerebrin, and kreatin.

ELECTRIC PROPERTIES OF NERVES.

Like muscle, nerves may be regarded as having a state of rest and a state of activity, but the two states are not obvious in the same striking way as they are in muscle, nor do we know much of the physical properties of nerve. While at rest, however, it shows electric phenomena similar to those which have already been described as belonging to muscle tissue. These electrical currents are contemporaneous with the life of the nerve, and they undergo the same variation as occurs in muscle when the nerve passes into the active state; that is, when it transmits an impulse.

The so-called *natural current* of nerve is practically the same as that of muscle, passing in the nerve to the central part from the cut extremities of the fibre; that is to say, the current passes through the galvanometer from the electrode applied to the middle of the nerve, to that applied to the extremity. The electro-motive force of a small nerve is much less than that of a muscle. In a frog's sciatic it has been estimated to be 0·02 of a Daniell cell. The natural current of the frog's nerve is said to increase in intensity in proportion to the increase in temperature up to about 20° C., after which it decreases.

Experiments on nerve currents must be carried on with all the precautions mentioned in speaking of muscle currents, and with the non-polarisable electrodes there figured (page 371).

The Active State of Nerve-Fibres.

Nerves pass into a state of activity in response to a variety of stimuli; their changed condition, however, cannot be readily recognized, because the only change we can detect in the nerve is that in its electric state. We soon know, however, when a nerve is conducting an impulse, if it be connected with its terminals. In the case of a nerve bearing impressions from the skin to the nerve centres, we get evidence of a sensation being felt, and when the nerve is motor—that is, bearing impulses from the centres to the muscles, we judge of the state of activity of the nerve by means of the muscle contraction which it brings about. For all ordinary experimental purposes we use the nerve of a frog with the muscle it supplies intact. This *nerve-muscle* preparation is commonly made from the leg of a frog, the sciatic nerve being carefully prepared from the thigh, while the gastrocnemius is cut away from all its attachments except that to the femur, which is retained as a point of fixation. In fact, the same method as is used for the indirect stimulation of muscle is employed for the study of the excitability of nerve-fibres.

NERVE STIMULI.

Besides the normal physiological impulse which comes from the cells in connection with the nerve fibres, they may be made to pass into the active state by a variety of stimuli, differing little from those which are found to affect muscle, when applied directly to that tissue. They may be enumerated as follows:—

1. *Mechanical stimulation.* Almost any mechanical impulse, applied to any part of a nerve, causes its excitation. The stimulus must have a certain degree of intensity, and have a definite, though it may be a very short, duration. If mechanical stimuli be frequently applied to a nerve in the same place, the irritability of the part is soon destroyed; but if fresh parts of the nerves be stimulated, at each blow the nerve passes into a state of tetanus, as shown by the contraction of the muscle to which it is supplied.

2. *Chemical stimulation.* First, must be named drying of the fibre, whether this be caused by ordinary evaporation, or facilitated with blotting paper, exposure over sulphuric acid, or the addition of solutions of high density, such as syrup, glycerine, or strong salt solution. Secondly, strong metallic salts or acids irritate nerves. Thirdly, alcohol and ether, and a solution of bile; and lastly, even weak alkalis, except ammonia, which has no effect on nerve, although it acts on muscle when applied directly to that tissue.

3. *Thermic stimulation* occurs when sudden changes are brought about approaching either of the extreme temperatures at which the nerve can act; *i.e.*, near 5° or 50° C.

4. *Electric stimulation* is by far the most important for physiologists, being the most delicate, most easily applied and regulated, and the least injurious to the nerve tissue. As was mentioned with respect to muscle, any sufficiently rapid change of intensity in an electric current passing through a nerve causes in it the molecular changes we call excitation, as evidenced by the muscle contracting, and the natural electric currents of the nerve undergoing variation. The less the absolute intensity of the current, the greater the effect any given change in intensity causes. The muscle of a nerve-muscle preparation contracts, when a weak constant current, say from a single small Daniell cell, is suddenly allowed to pass through the nerve. This is done by placing a part of the nerve in the circuit, which is made complete, by closing a key, when the stimulation is to be applied. This form of stimulation is called a *making shock.* While the current is allowed to pass through the nerve no

effect is produced if the battery be quite constant. On breaking the circuit by opening the key the current suddenly ceases, and another contraction occurs, this is called the *breaking shock*. At each making and breaking of the constant current, a stimulus is applied to the nerve, and transmitted to the muscle, and it has been found that a weaker current suffices to bring about a contraction when applied to the nerve, than when it is applied to the muscle directly.

If a strong constant current be allowed to pass through a considerable length of a nerve for some little time, and the circuit be then suddenly broken, instead of a single contraction tetanus of the muscle results. This *breaking* tetanus (Ritter's tetanus) is easily produced when the positive pole or anode is next the muscle. Sometimes in particular conditions of the nerve, and with certain strengths of stimulation, a *making* tetanus also occurs, but more rarely and only when the negative pole is next the muscle.

When a constant current, such as we get directly from a Daniell cell, is used, that part of the nerve between the stimulating points, through which the current passes is found not to be equally affected throughout its entire length, but one single point is stimulated whence the impulse spreads. This may be the point where either of the poles is in contact with the nerve; and further, a different pole starts from the stimulus, according as the circuit is made or broken. With a *making shock* the stimulation takes place at the negative pole or cathode, and with a *breaking* shock at the positive pole or anode. That is to say the point where the current leaves the nerve is affected at the *make*, and the point where the current enters the nerve is affected at the break of the current.

It has also been found that, other things being equal, the making shock is a more powerful stimulus than the breaking shock; *i.e.*, a weak current will sooner cause a contraction when the circuit is made than when it is broken.

This remarkable fact that the impulse starts from the anode in a breaking shock is proved by means of the *breaking tetanus* just alluded to. It has been found that when the positive pole or anode is next to the muscle the breaking tetanus lasts longer and is stronger than when the anode is placed at a greater distance from the muscle than the cathode; and further, when the anode is beyond the cathode section of the nerve in the intrapolar region, during stimulation the tetanus stops it at once, because the point from which the stimulus comes is thereby cut off from the muscle. Section has no effect if the anode be next the muscle, the tetanus proceeding in a normal way, only the inactive pole being cut away from the muscle.

That the stimulus occurs at the cathode in a making current may also be demonstrated by the fact that it takes a certain measurable time for the impulse to travel along the nerve. If then the cathode be placed far from the muscle and the anode near it, the contraction after a *breaking shock*, when the stimulus starts from the anode, will occur sooner than that which follows the *making*, when the stimulus starts from the cathode, because the impulse has a less distance of nerve to traverse in the former case.

In ordinary experiments on nerve, a constant current, *i.e.*, one coming directly from a battery, is seldom used, because there is no means of regulating or varying the strength of the stimulation, and it is not convenient to *make* and *break* the current in order to excite the tissue continuously. And further, the more rapid current *induced* in one coil of wire—the secondary coil—by the making or breaking of a current passing through another coil—the primary coil—is more effective and suitable for physiological purposes. The strength of the induced current being approximately in inverse proportion to the square of the distance between the two coils—moving the secondary away from the primary coil gives a ready means of varying and regulating the strength of the stimulus without any special care being devoted to the exact strength of the element used.

DuBois Reymond's Inductorium is the instrument commonly used in physiological laboratories. In it the secondary coil can be moved away from the primary on a slide which is graduated, and the primary current may be made to pass through a magnetic interrupter so as to cause a rapid succession of breaks and makes, and thus give a series of stimulations one after another, which is necessary in order to produce tetanus. A drawing and further description of the instrument will be found at p. 376.

VELOCITY OF NERVE FORCE.

It has already been stated that nerve fibres are capable of conducting impulses in either direction—from or to the nervous centres—the position and the character of the terminal organs determining the direction in which the nerve force usually travels. In the ordinary peripheral nerves there are generally both kinds—efferent and afferent fibres carrying impulses in different directions without interfering with one another.

When we reflect that the passage of an impulse along a nerve is brought about by a molecular change in the axis cylinder, we are at once struck with the rapidity with which impressions are transmitted from one part of the body to another. This surprising velocity is, however, only relatively great. When we compare it with the velocity of the electric current or of light, we at once see how incomparably slower the rate of nerve impulse is, and that it may, with more advantage, be compared with rates of motion commonly under our observation. To take every-day examples :—*viz.*, nine metres per second is about as fast as the quickest runner can accomplish his 100 yards ; race-horses can gallop about 15 metres a second for a mile or so ; a mail train at full speed travels at about 30 metres a second, and the velocity of nerve force has been estimated to be in cold-blooded animals 27 metres per second ; and in man about 33 metres per sec. So that the intercommunications between man's brain and the various parts of his body only travel about the same rate as an express train, and about twice as fast as the quickest horse can gallop.

In order to measure the rate of transmission of nerve force, different methods may be employed ; the simplest of which is to make a muscle draw two curves one over the other, with a good myograph such as described in Chap. XVI., p. 382, in one of which the stimulation is applied to the nerve close to the muscle, and in the other, as far as possible away from the muscle. The difference in length of the latent period, as estimated by the tuning-fork tracing, corresponds to the time the impulse has taken to travel along the part of the nerve between the two points of stimulation.

Utilising the fact that the extent of deflexion of the needle of a galvanometer is in proportion to the duration of a current of known strength passing through it for a short time, an accurate measurement of the difference in time, of remote, and near or direct stimulation of a nerve, may be made. By a special mechanism the time-measuring current is sent through the galvanometer at the same moment that the stimulating current goes through the nerve, and the instant the muscle begins to contract, it breaks the current passing through the galvanometer, so that this time-measuring current lasts only from the moment when the nerve is stimulated until the muscle begins to contract.

THE ELECTRIC CHANGE IN NERVE.

Negative Variation.—The natural current of a nerve, like that of muscle, undergoes a diminution at the moment the nerve is stimulated ; this is termed the *negative variation.* It occurs with any other form of stimulation as well as when an electric shock is used, so it is not dependent on an escape of the stimulating current. In the case of a single stimulation, the negative variation is so rapidly over—lasting only ·0005 sec., that the inertia of the needle of the galvanometer prevents the change in the current being indicated. In tetanus, however, it makes a decided impression on the galvanometric needle. The strength of the negative variation depends on the condition of the nerve and the strength of the stimulus; being stronger when the nerve is fresh and irritable and has a good natural current, and when a strong stimulus is applied.

The negative variation of the natural currents passes along the nerve from the point of stimulation in both directions, just as does the nerve impulse; and with a galvanometer the electric change may be traced from the nerve to the muscle. Moreover, it has been made out that the negative variation travels along the nerve at just the same velocity as the impulse does from the point of stimulation; namely, about 27 metres per second; and further, this rate is said to be influenced in the same way by the passage of a constant current through the nerve (to be presently described) as is the impulse derived from stimulus. These points seem to lead to the belief that the nerve impulse and the negative variation are identical. This peculiar electric change and its accompanying impulse pass then along the nerves as a kind of wave of activity, the *speed* and the *duration* of which we know to be 27 metres per sec. and ·0005 of a sec. respectively; the length of the wave we therefore calculate to be about 18 millimetres.

ELECTROTONUS.

If the two poles leading to a galvanometer be applied to the centre, and to the end of a nerve respectively, so as to indicate the natural current, and at the same time another part of the nerve be placed in the circuit of a constant current from a battery, when the circuit of the constant (now called *polarising*) current is completed, a change is found to take place in the natural current; this is called *electrotonus*. Instead of the natural currents from the *equator* to the *pole* of the nerve, a current is found to pass through the entire length of the nerve in the same direction as the polarising current from the battery. This electrotonic current is not proportional to the strength of the natural currents, and is to be recognised when the latter are no longer to be found. The electrotonic current is stronger with a strong polarising current, and is most marked in the immediate neighbourhood of the poles fading gradually away as one passes to the remoter parts of the nerve. The electrotonic state is not to be attributed to an escape of the constant polarising current, because it decreases gradually with the waning of the physiological activity of the nerve, and ceases at the death of the nerve long before the tissue has lost its power of conducting electric currents. Moreover, it has been shown that a ligature applied to the nerve so as to destroy its physiological continuity, but not its power of carrying electric currents, prevents the electrotonic current passing to the part of the nerve which is thus separated.

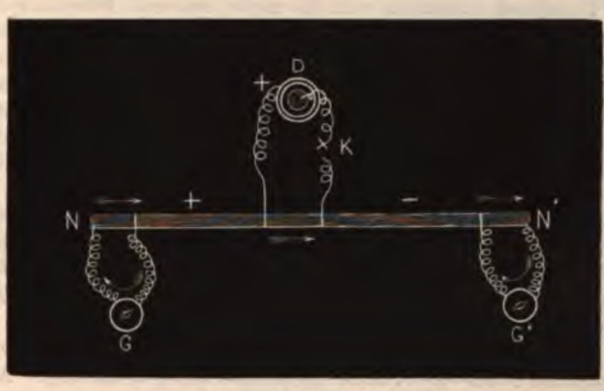


Fig. 202.—Diagram to illustrate Electrotonus.

N. N'. Portion of Nerve. G. G'. Galvanometers. D. Battery from which polarising current can be sent into nerve by closing key K. The direction of the polarising and electrotonic currents is indicated by the arrows, and is seen to be the same.

The condition of the portion of the nerve near the anode—positive *pole*—is found to differ somewhat from that near the cathode—negative pole—and hence it is found convenient to speak of the region of the anode being in the *anelectrotonic*, and that near the cathode being in the *catelectrotonic* condition. A certain time is required for the production of *anelectrotonus* and *catelectrotonus*, a current of less duration than ·0015 of a second being unable to bring about the change; the negative variation is, therefore, over before the electrotonus has commenced.

IRRITABILITY OF NERVE FIBRES.

The irritability of nerves varies according to certain conditions and circumstances. While uninjured in the body, the irritability of a nerve depends *upon*—

1. A perfect supply of blood so as to bear to it the necessary quantity of new material as nutriment, and to carry off any injurious effete matters that may be produced by its molecular changes.

2. A suitable amount of rest. Prolonged activity causes fatigue and loss of irritability, no doubt from the same causes as were mentioned as bringing about fatigue in muscles. The chemical changes taking place in nerves, however, have not yet been made out with any degree of accuracy.

3. Uninjured connection with the nerve centres. When a spinal nerve is cut, the part connected with the periphery rapidly undergoes degenerative changes which seem to depend upon faulty nutrition, since they are accompanied by structural changes—fatty degeneration. This appears to commence in a very short time after the section—commonly in about five days. The part of the nerve remaining in direct connection with the cord, retains its irritability for a very much longer time.

In the artificial stimulation, by means of electric shocks applied to the nerve of a cold-blooded animal, there are many minor conditions which have considerable influence on the irritability, as evidenced by the response given by the attached muscle to weak stimuli. The more important of these are :—

1. Temperature changes. In the case of a frog's nerve, a rise of temperature to 30—40° C. causes an increase in its excitability. Also a fall of temperature below zero tends to make the nerve more easily excited. Both these conditions have, however, a very fleeting effect, for the nerve soon dies at the temperatures named, and most probably the increased irritability is only to be taken as a sign of approaching death. It thus appears that a medium temperature is the optimum for nerve work.

2. The part of the nerve stimulated, is also said to have some effect on the result of a given strength of stimulus. The further from the muscle, the more powerful the contraction produced, other things being equal. So that the impulse is supposed to gather force as it goes, as in the case of a falling body, and hence has been spoken of as the *avalanche* action of nerve impulse.

3. A new section of the nerve is said to increase its irritability, as does, indeed, any slightly stimulating influence, such as drying, and chemical or mechanical meddling of any kind. This increase in irritability probably depends upon injurious changes going on in the nerve, as the influences just alluded to lead to complete loss of *excitability* if carried too far.

4. The most remarkable change in the excitability of a nerve,

is that brought about by the action of a constant current passing through the nerve, so as to set up the conditions just described as anelectrotonus and catelectrotonus. (*a*) The irritability of the nerve is considerably increased in the region near the cathode, and it is notably diminished in the neighbourhood of the anode.

(*β*) The increase of irritability is in proportion to the intensity of the catelectrotonic state, and the decrease in proportion to the intensity of the anelectrotonus. Thus the increase is most marked in the immediate neighbourhood of the cathode, and fades with the distance from the negative pole ; and similarly, the decrease is strongest at the anode, and becomes less and less as it passes away from the positive pole. In the same way, in the part of the nerve between the two poles—the intrapolar region—the decrease and increase of irritability become less marked towards the middle point, between the cathode and the anode, so that here we find an unaffected part, which has been called the *indifferent point.*

It is a remarkable fact that this indifferent point is not always midway between the two poles, but decreases its distance from the cathode in proportion as the polarising current is made stronger. That is to say (γ), with strong polarising currents the indifferent point is near the cathode (B) ; with weak currents it lies near the anode (A) (Fig. 203).

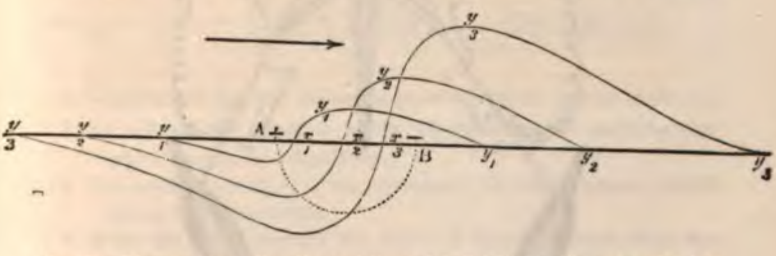


Fig. 203.—Diagram illustrating the variations of irritability of different parts of a nerve during the passage of polarising currents of varying strength through a portion of it.

A = Anode ; B = Cathode ; AB = Intrapolar district ; y^1 = Effect of weak current. y^2 = Effect of medium current. y^3 = Effect of strong current.

The degree of effect is shown by the distance of the curves from the straight line. The part of curve below the line corresponds to *decrease*, that above to *increase* of irritability. Where the curves cross the line is called the indifferent point. With strong currents this approaches the cathode. (From Foster after Pflüger.)

Besides becoming less irritable in proportion as the polarising current becomes more powerful (δ), the anelectrotonic region of the nerve loses its ability to conduct impulses, and may finally, with a very strong current, even when applied for a short time, become quite incapable of conducting an impulse.

If the polarising current be now opened, so as to stop its passage through the nerve, and remove the anelectrotonic and the catelectrotonic states (ε), a kind of rebound occurs in the condition of both the altered regions, and the part which has just ceased to be catelectrotonic, and was, therefore, over-irritable, becomes, by a kind of negative modification, very much lowered in its irritability; while on the other hand, the anelectrotonic part, by a positive rebound, becomes more excitable than in its normal state. The rebound over the line of normal irritability lasts but a very short time; but still, as we shall see presently, it is of greater duration than the passage of the negative variation along the nerve.

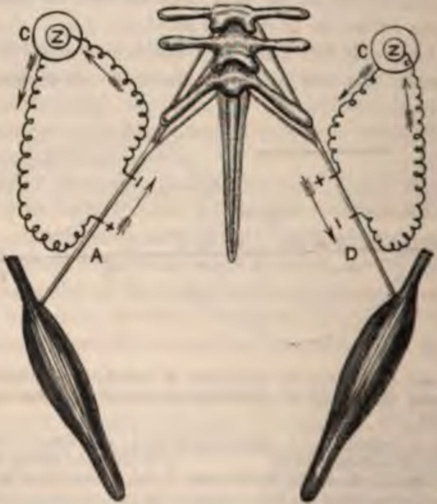


Fig. 204.—Diagram showing the meaning of the terms *ascending* and *descending* currents, used in speaking of the law of contraction. The end of the vertebral column, sciatic nerves, and calf muscles of the frog are shown, while the arrows indicate the direction of the ascending current A, on the left, and the descending current D, on the right, according as the positive pole C of the battery is below or above.

LAW OF CONTRACTION.

Upon the foregoing facts (*a*—ε), and others already mentioned—*viz.*, that the impulse starts in the nerve from different poles and with different force, with a making and a breaking shock—depends the law of contraction, which would be difficult to understand without bearing in mind all these interesting points.

It was found that, with the same strength of stimulation, not only were different degrees of contraction produced with making and breaking shocks, but also that, other things being similar, a different result followed when the current was sent through the nerve in an upward direction (*i.e.*, from the muscle), and when it was sent in a downward direction (*i.e.*, towards the muscle). The stimulating current is spoken of, in the former case, as an *ascending current*, and in the latter as a *descending current.*

The following is a tabular view of the law of contraction :—

	Ascending Currents.	Descending Currents.
Weak Stimulation.	Make = Contraction. Break = No response.	Make = Contraction. Break = No response.
Medium ,,	Make = Contraction. Break = Contraction.	Make = Contraction. Break = Contraction.
Strong ,,	Make = No response. Break = Contraction.	Make = Contraction. Break = No response.

To explain this law the following points must be kept in view :—

1. In a breaking shock, it is the *disappearance* of *anelectrotonus* which causes the stimulation.
2. In a making shock it is the *appearance* of *catelectrotonus* which causes the stimulation.
3. With the same current the *make* is more powerful than the *break.*
4. Anelectrotonus causes *reduction* of irritability and conductivity.
5. Catelectrotonus causes *increase* of irritability.
6. With *ascending currents* the part of the nerve next to the muscle is in a state of reduced functional activity (anelectrotonus).
7. With *descending currents* the part of the nerve next the muscle is in a state of exalted activity (catelectrotonus).
8. The reduction or exaltation of activity is much greater with strong currents.

That only making shocks cause contraction with very weak currents, simply depends on the greater efficacy of the entrance of catelectrotonus into the nerve, which causes the making stimulation.

That contraction follows in all four cases, with medium stimulation, is explained by assuming that the depression of the functional activity of the nerve is not sufficient to affect its conductivity.

The want of response to a making shock, in the case of the strong descending current, depends upon the fact that the part of the nerve near the muscle, around the anode, is in a state of lowered activity. and is, therefore, unable to conduct the impulse which has to pass through this region from the cathode, where the stimulation takes place, in order to reach the muscle.

The absence of contraction at the breaking of a strong descending current, is caused by the same lowering of the conductivity of the nerve between the point of stimulation and the muscle, because at the cessation of strong catelectrotonus, the region near the cathode rebounds from exalted to depressed activity, and at the moment of stimulation the greater part of the intrapolar region is an electrotonic.

The specific use of nerve fibres in the body of the higher animals may be thus briefly stated. They form a means of extremely rapid intercommunication between distant parts. The protoplasm of the axis cylinder has undergone a special modification, by which it is enabled to conduct impulses much more quickly than ordinary protoplasm does. Even the most nearly-related substance, muscle tissue, transmits impulses about thirty times more slowly than a nerve fibre. A highly organised animal body, without nerve fibres, would be in a worse condition than a highly organised state without a telegraph or even a postal system.

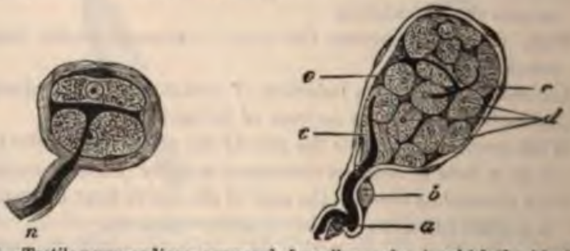


Fig. 205.—Tactile nerve endings, composed of small capsules, in which the black axis-cylinder of the nerve (*a*), and (*n*) meets with many protoplasmic units.

Nerve Corpuscles or Terminals.

These are the real actors in the nervous operations, while the fibres are merely their means of communicating with one another. One great set of terminals is placed on the surface of the body and is adapted to the reception of the various external influences which are brought to bear on it from without by its surroundings. These receivers of extrinsic stimuli are necessarily much varied so as to be capable of appreciating all the different kinds of stimulation presented to them. They are either distributed over the entire surface so as to meet with general mechanical and thermic changes, or they are further specialised for the reception of luminous, sonorous, odorous or gustatory impulses. In the latter cases the special terminals are collected into one part, and usually form complex organs, which will be described presently in the chapters on the special senses. Another great set of terminals are placed in the deeper textures, when they act as local distributing agents; such as the nerve plates on skeletal muscles, and the ganglionic networks in the wall of the intestine. In many instances, however, the exact mode of connection between the nerve and the protoplasm of the tissue elements, to which it bears impulses, has not been satisfactorily made out. In the remaining class of nerve terminals the cells are grouped together so as to form larger and smaller colonies, and more definitely deserve the name of nerve or ganglion cells. These are the central terminals, and are placed either in the cerebro-spinal axis, or in swellings of the nerves called sporadic ganglia.

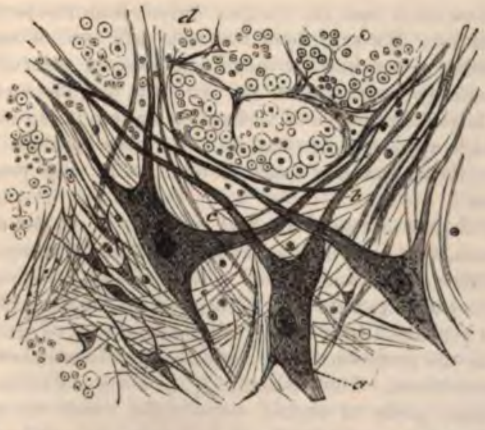


Fig. 205*.—Multipolar cells from the anterior grey column of the spinal cord of the dog-fish (*a*) lying in a texture of fibrils; (*b*) prolongation from cells; (*c*) nerve-fibres cut across. (Cadiat.)

Of these nerve cells there are many varieties, all of which have the following characteristics. The cells are of considerable size and have processes branching off from them, by means of which they communicate with the nerve fibres. These processes may be single or many, hence they are spoken of as uni,- bi-, or multipolar cells, &c. The nucleus is commonly very distinct, and contains a well-marked nucleolus. The abundant protoplasm, which is usually contained in a delicate cell wall, is in direct connection with the axis cylinder of the nerve fibres, with which it communicates by means of thin strands of protoplasm that pass out from the cell by the processes. A delicate striation of the protoplasm may sometimes be recognised, indicating the course of the nerve fibrils as they run into the cells from the processes.

THE FUNCTIONS OF NERVE CELLS.

Any mass of living protoplasm, such as an amœba, can receive extrinsic impulses, which affect directly its conditions, and though the impression may be very localised in its application, yet all the parts of the cell participate in the sensation, and probably take part in the resulting movement.

Besides those acts of which we can recognise the cause, many others occur in an amœba which we are not able to trace to any definite cause other than the energies derived from its special powers of assimilation. We say, then, that not only can an amœba feel local stimulation, transmit the impulse to remoter parts of its body, and respond by movement to the stimulus, but, moreover, as the result of intrinsic processes of a chemical nature, it can initiate impulses which appear as motions, &c. We may conclude from this fact alone that automatic action is one of the vital properties of protoplasm.

Now in the nerve centres we find, certainly in all the more complex animals, that each of these kinds of action is commonly distributed, so that different individual cells have each a different act to perform, and thus an important division of labour takes place. The first act is performed by a wonderfully elaborate set of special organs adapted to the reception of the various extrinsic impulses or sensations from without. The excitation is then sent by nerve fibres to another great group of central nerve cells, which are apparently employed solely in receiving the stimuli from the peripheral organs, and then distributing the impulses to their neighbours, which can direct, modify, analyse, classify, re-distribute, or check the impulses, so that other nerve cells may have the least possible amount of trouble, and at the same time lose none of the advantage that is to be gained from the income derived from stimulus coming from without. Connected with the last group is another, the nerve cells which lie out of the reach of the ordinary peripheral impulses, but are capable of developing within themselves energies, and can initiate impulses with no other aid than that of their nutrition and the chemical changes resulting from their assimilation.

These impulses are distributed to the peripheral active tissues, muscles, glands, &c., probably through the medium of other sets of cells analogous to the last group situated in the nerve centres as well as to the local distributors which act as unions between the other textures and the nerve fibres.

The functions of these nerve cells which form centres of action may be classified thus :—

1. Reflexion. Many nervous cells are capable of reflecting an impulse received by an afferent nerve ; that is to say they send it by an efferent nerve to some active tissue, such as a muscle or gland. This kind of direction is spoken of as a simple *reflex action*. For instance, if a grain of red pepper be placed on the tongue, the stimulus soon travels from the peripheral receiving terminal, along an afferent nerve to its central terminal, which reflects the impulse to the efferent nerve, going to the salivary gland, and the result is an increased secretion of saliva.

2. Co-ordination. There are but few reflex acts that do not require the co-operation of several cells, and these work together in an orderly manner, the resulting activity being well arranged and usually adapted to some purpose. The first act of the receiving cells of this reflex centre must then be to distribute and direct the impulse into those channels which lead to groups of cells capable of sending impulses in an orderly and definite direction. This directing and arranging power is spoken of as *co-ordination*, and probably is an attribute common to all nerve cells.

3. Augmentation. Usually the force of the reflected efferent impulse bears a direct relation to the afferent impulse as determined by the strength of the stimulus. Thus if the amount of pepper on the tongue be much increased, not only is the flow of saliva greater, but the stimulus spreads from one central cell to another until the neighbouring centres are affected. Thus we often find the lachrymal glands are also influenced by very strong stimulation of the tongue, and pour out their secretion, as is said, "in sympathy" with the mouth glands. But the amount of the afferent impulse is not

the only factor in determining the amount of response to be reflected along the efferent channels. Some nerve cells have a distinct power of increasing the amount of response to be given to a given stimulus. When an irritant falls near the laryngeal opening, a very different effect is produced, and the vastly greater response to an equal stimulus depends rather on the *augmenting* power of some central cells than upon any greater sensibility of the local mechanisms.

4. Inhibition.—Under certain circumstances, such as pre-occupation, &c., which will be more fully explained presently, nerve cells withhold the transmission of a stimulus, or lessen the impulse reflected so as to produce little or no effect, this is called *inhibition*.

5. Automatism.—Nerve cells are supposed to have the power of originating impulses; *e.g.*, those carrying on operations which require to be of a more or less permanent kind, such as the closure of the sphincter muscles and the partial contraction of the muscle cells of the arteries. *Automatic actions* are sometimes spoken of as those that are continuous and those that undergo rhythmical changes. If carefully examined, however, most of the so-called constant automatic nervous actions will be found to show some traces of rhythmic relaxation. Nerve cells, with automatic properties, may be exercised in preventing reflex actions having their full effect, and thus they act as aids to the controlling part played by the reflex cells. And in the same way automatic cells may be influenced and even regulated by impulses coming from the periphery to reflex centres in the vicinity, which join forces with the automatic centre. Thus the act of respiration may be performed by pure automatism, and its centre supplies a good example of an automatic group of cells. As a matter of fact, however, the respirations are regulated by a reflex mechanism, the channels of which reside in the vagus nerve.

Moreover it is in the nerve cells that we must seek mental activity, under which term may be considered perception, volition, thought, and memory. It is very difficult to allocate the due proportions of reflexion, co-ordination, augmentation, inhibition, automatism, &c., requisite for the development of what we must call mental faculties, but there can be no doubt that the mind must be the resultant of a long series of external and internal excitations, modified by intrinsic influence, and acting upon innumerable groups and masses of nerve cells, the general outline of which has been rough-hewn by hereditary tendency.

CHAPTER XXIX.

SPECIAL PHYSIOLOGY OF NERVES.

SPINAL NERVES.

THE thirty-one pairs of nerves which leave the vertebral canal by the openings between the vertebræ are called spinal nerves, in contradistinction to the cranial nerves, which come out through the base of the skull. They are attached to the spinal marrow by two bands, the anterior and posterior "roots," which unite together in the intervertebral canal to form the trunk of the nerve. Just before the junction of the two roots the posterior one is enlarged by a ganglionic swelling.

The spinal nerves are all "mixed nerves," that is to say, they contain both efferent and afferent fibres; but these two sets of fibres run separately in the anterior and posterior roots of each nerve. The spinal nerves are thus joined to the spinal marrow by two nervous cords, each one of which contains only efferent or afferent channels. About seventy years ago Charles Bell discovered that the anterior roots carry the efferent fibres and the posterior the afferent. Hence, the anterior are commonly spoken of as the *motor roots*, and the posterior as the *sensory roots* of the spinal nerves. The experiment to show this difference is simple, but requires very delicate manipulation. If the anterior roots of the nerves supplying the hind leg of a recently-killed frog be divided, the muscles of the limb are cut off from the centres in the spinal cord, and therefore the leg hangs limply, and does not move if it is pinched when the frog is suspended; whereas the limb on the sound side, upon which the anterior roots are intact, will move energetically when the motionless one is irritated. If the distal ends of the divided anterior roots be stimulated, the muscles of the paralysed limb are thrown into action; but stimulation of the proximal end gives no result. Further, if the two webs of this frog be compared, the blood-vessels running across the transparent part of the web on the injured side will be found to be fuller than those in the web of the other limb, but if the distal ends of the motor roots are stimulated, the dilated blood-vessels return to their normal calibre. By these experiments we are shown that, together with fibres to the skeletal muscles, efferent fibres carrying impulses to the muscular walls of the vessels are contained in the anterior roots of the spinal nerves.

The fact that when the leg on the side where the anterior roots have been severed is stimulated, moves the other, is sufficient to show that the sensory connections between its surface and the cord are not destroyed by cutting those anterior roots; and we may conclude—taking the other facts just mentioned into account—that the afferent fibres are situated in the posterior roots.

We can confirm this result by cutting the posterior roots on one side of a recently-killed frog, and repeating the stimulation of the feet.

Pinching the limb whose posterior roots are cut, gives rise to no response, because the impulses cannot reach the spinal cord; but stimulation of the sound foot causes obvious movements of both legs. This shows that the section of the posterior roots of one limb cuts off the afferent (sensory) communication on the side operated on, but that the efferent (motor) impulses can pass freely to the muscles, even when the posterior roots are divided, for the limb moves on pinching the other foot. Further, if the proximal ends of the cut posterior roots be stimulated, motions are produced showing that the centres in the spinal cord are influenced by the afferent impulses carried by those posterior roots. On the other hand, if the distal ends of the cut roots be stimulated no movement results.

It has been sometimes found that stimulation of the anterior roots seemed to cause pain, as shown by the motion of other parts besides those to which this root was itself distributed; and it was believed that some sensory fibres must run in the anterior roots. But it has been since found that if the posterior roots be first cut these signs of pain are not shown when the anterior roots are stimulated. From this it has been concluded that the apparent sensory channels of the motor roots are nothing more than some sensory fibres which pass from the nerve trunk a little way up the motor root, and then turn back and descend again to the junction of the roots, whence they pass along the posterior root to the cord. These fibres are named the "recurrent sensory fibres," and the recurrent sensibility of the anterior roots is not regarded as any serious departure from Bell's law.

The course of the secretory, &c., nerves probably follows that of the motor channels at their exit from the cord. Their peripheral ditribution, and that of the vaso-motor nerves, are intimately connected with the sympathetic system, and will be considered further on

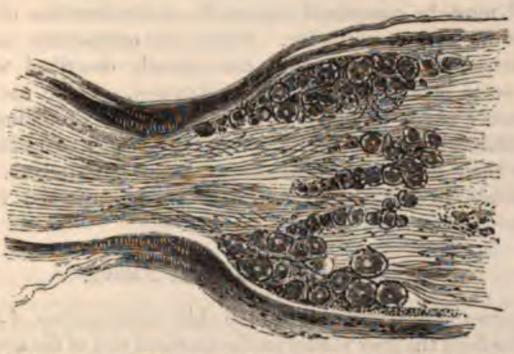


Fig. 206.—Section through spinal ganglion of a cat, showing ganglion cells interspersed between the fibres. (Low power.)

Of the function of the ganglia on the posterior roots of the spinal nerves but little is positively known. There is no evidence of their being centres of reflex action, nor can they be shown to possess any marked automatic activity. From the fact that when a mixed nerve is divided the end cut off from the ganglion degenerates after a few days, these ganglia are supposed to preside over the nutrition of the tissue of the nerve itself. And if the roots be cut, that part of the posterior root attached to the cord degenerates, while the piece connected with the ganglion is well nourished. This is not the case if the anterior root be divided, but, on the contrary, that portion next the cord is well nourished, while that going to join the posterior root is degenerated.

It would thus appear that the trophic function of the ganglia is restricted to the sensory nerves, while the nutrition of the motor nerves is provided for by nervous centres situated higher up.

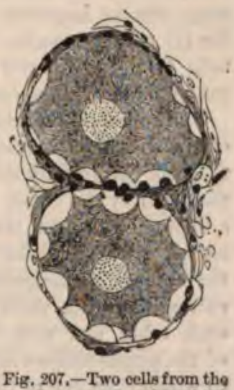


Fig. 207.—Two cells from the former seen under a high power, showing the fine protoplasm here and there retracted from the cell-wall.

THE CRANIAL NERVES.

The nerves which pass out through the foramina in the base of the skull must be considered separately, as the function of each of them shows some peculiarity. Some are exclusively nerves of special sense, and may be most conveniently described when the special sense organs are under consideration. Some are simple, being purely motor in function, while others are exceedingly complex, containing many kinds of fibres. They may be taken in the order of their functional relationships, motor and mixed. Those which relate to the special senses will be considered in future chapters.

III.—THE MOTOR OCULI NERVE.

The nerves of the third pair are the chief motor nerves of the eyes. They arise from the grey matter on the floor and roof of the aqueduct of Sylvius, and pass out of the brain substance near the pons from between the fibres of the peduncle, and then run between the posterior cerebral and superior cerebellar arteries. They pass into the orbits in two branches, and are distributed to the following orbital muscles :—(1) elevator of the eyelid ; (2) the superior, (3) inferior, and (4) internal recti, and (5) the inferior oblique. They also contain fibres which carry efferent impulses to the (1) circular muscle of the iris, and to the (2) ciliary muscle. The latter branches reach the eye by a short twig from the inferior oblique branch, which goes to the ciliary ganglion, and thence enter the ciliary nerves.

The action of the orbital muscles is, in the main, under the control of the will, though they afford good examples of peculiar co-ordination and involuntary association of movements. The contraction of the pupil by the action of the circular muscle (sphincter pupillæ) is a bilateral reflex act, the afferent impulse of which originates in the retina, passes along the optic nerves, and is transmitted, probably in the corpora quadrigemina, to both the third nerves. The central extremities of the third nerves must have an intimate connection with each other and with the optic nerves, for the diminution in size of the pupils follows accurately the increase in intensity of the light to which even one of the retinæ is exposed. In retinal blindness and after section of the optic nerve the pupil is dilated. The action of the ciliary muscle may be said to be voluntary, since we can voluntarily focus our eyes for near or far objects. Contraction of the *sphincter* pupillæ and of the internal rectus is associated with the contraction of the ciliary muscle in accommodation.

Injury or disease of the third nerve within the cranium gives rise to the following group of phenomena :—(1.) Drooping of the upper lid (Ptosis). (2.) Fixation of the eye in the outer angle (Luscitas). (3.) Dilatation and immobility of pupil (Mydriasis). (4.) Inability to focus the eye for short distances.

IV.—THE TROCHLEAR NERVE.

This thin nervous filament arises under the Sylvian aqueduct, and passes into the superior oblique muscle, to which it carries voluntary impulses, which are involuntarily associated with those of the other muscles moving the eyeball. Paralysis of this muscle causes no very obvious impairment in the motions of the eyeball when the head is held straight, but it is accompanied by double vision, so there must be some displacement of the eye-ball. When the head is turned on one side the eye follows the position of the head instead of being held in its primary position. In paralysis of this nerve a double image is seen only when looking downwards, and the image on the affected side is oblique and below that seen by the sound eye.

VI.—THE ABDUCTOR NERVE OF THE EYE.

This arises in the floor of the fourth ventricle, and appears just below the pons Varolii. It is the motor nerve of the external rectus muscle of the eye. Paralysis or section of it causes internal squint.

VII.—(PORTIO DURA) MOTOR NERVE OF THE FACE.

This nerve arises from a grey nucleus in the floor of the fourth ventricle. It passes with the other part of the seventh (portio mollis) or auditory nerve into the internal auditory meatus of the temporal bone. It first passes out towards the hiatus, and then turns at a right angle to form a knee-like swelling (geniculate ganglion), and then runs backwards along the top of the inner wall of the drum, and passing downwards through a special canal in the bone, comes out at the stylo-mastoid foramen, and finally spreads out on the side of the face. It is essentially an efferent nerve, being partly motor and partly secretory, though its connections have caused afferent functions to be ascribed to it. Its distribution may be thus briefly summarised :—

i. *Motor fibres.*—(1.) To the muscles of the forehead, eyelids, nose, cheek, mouth, chin, outer ear, and the platysma, which may be grouped together as the muscles of expression. (2.) To some muscles of mastication, viz., buccinator, posterior belly of digastric, and the stylohyoid—all the foregoing being supplied by external branches—while in the temporal bone it gives a branch to (3) the stapedius muscle, and also a branch from the geniculate ganglion named the great superficial petrosal nerve, which after a circuitous course is supplied to the elevator and azygos muscles of the palate and uvula.

ii. *Secretory fibres.*—(1.) To the parotid gland by the small superficial petrosal nerve, which sends a branch to the otic ganglion, whence the fibres pass to the auriculo-temporal nerve, and then on to the gland. (2.) To the sub-maxillary gland by the chorda tympani, which after traversing the tympanum leaves the ear by a fissure at its anterior extremity, then joins the lingual branch of the fifth to separate from it and pass into the sub-maxillary ganglion which lies in close relation to the gland (compare figs. 64 and 65).

iii. Vaso-motor, or vaso-inhibitory influences, are chiefly connected with the secretory function, since dilatation of the vessels of the glands accompanies the increased secretion that follows stimulation of the nerves going to the glands.

iv. The following afferent impulses are said to travel along the track of the portio dura and its branches:—(1.) Special taste-sensations, which are chiefly located in the chorda tympani branch, may be explained by the branches of communication which pass from the trunk and petrous ganglion of the glosso-pharyngeal to the portio dura at its exit from the foramen, or by the connection in the drum of the ear between the tympanic branch of the glosso-pharyngeal and the geniculate ganglion of the portio dura through the lesser superficial petrosal nerve. (2.) Ordinary sensations, which are also located in the chorda tympani, are said to traverse this nerve in an afferent direction until it comes near the otic ganglion, when the sensory fibres leave the chorda and pass to the inferior division of the fifth nerve through the otic ganglion.

Injury of the facial nerve in any of the deeper parts of its course gives rise to the striking group of symptoms known as facial paralysis, the details of which are too long to be given here. When it is remembered that muscles aiding in expression, mastication, deglutition, hearing, smelling, and speaking, are paralysed, and that taste, salivary secretion, and possibly ordinary sensation are impaired, one can form some idea of the complex pathological picture such a case presents.

V.—N. TRIGEMINUS, OR TRIFACIAL NERVE.

This nerve transmits both efferent and afferent impulses, which, however, are carried by two different strands of fibres. The motor part, which arises from a grey nucleus in the floor of the fourth ventricle, is much the smaller of the two, and has been compared to the anterior root of a spinal nerve. The large sensory division springs from a very extensive tract, which can be traced from the pons Varolii through the medulla to the lower limit of the olivary body, and on to the posterior cornua of the spinal marrow. This set of fibres has been likened to the posterior root of a spinal nerve, being somewhat analogous to it in origin, function, and the fact that there is a large ganglion on it within the cranium.

The distribution and peripheral connections of this nerve are somewhat complicated, and should be carefully studied when the manifold functions of its branches are being considered. The various impulses conveyed by the tri-facial nerves may be thus enumerated :—

i.—EFFERENT FIBRES.

1. *Motor.*—To the muscles of (1) mastication, viz., temporal masseters, both pterygoids, mylohyoid, and the anterior part of the digastrics ; (2) to the tensor muscle of the soft palate ; and (3) to the tensor tympani. (4) In some animals (rabbit) nerve filaments also pass to the dilator muscle of the iris, reaching the eyeball by the ciliary ganglion.

2. *Secretory.*—The efferent impulses which stimulate the cells of the lachrymal gland to increased action, pass along the branches of the ophthalmic division of this nerve.

3. *Vaso-motor.*—The nerves governing the muscles of the blood vessels of the eye, of the lower jaw, and of the mucous membrane of the cheeks and gums.

4. *Trophic.*—On account of the impairment of nutrition of the eye and the mucous membrane of the mouth, which occurs after injury of the fifth nerve, it is said to carry fibres which preside over the trophic arrangements of these parts.

ii.—AFFERENT FIBRES.

1. *Sensory.*—All three divisions of the tri-facial nerve may be said to terminate in cutaneous nerves, by which the ordinary sensory impulses are carried from—(1) the entire skin of the face, and the anterior surface of the external ear ; (2) from the external

auditory meatus; (3) from the teeth and the periosteum of the jaws, &c.; (4) from the mucous membrane lining the cheeks, the floor of the mouth, and the anterior part of the tongue; (5) from the lining membrane of the nasal cavity; (6) from the conjunctiva, the ball of the eye, and the orbit generally; (7) and from the dura mater including the tentorium.

2. *Excito-motor.*—Some of the fibres which have just been enumerated as carrying ordinary sensory impressions, have special powers of exciting co-ordinated reflex motions. Thus the sensory fibres from the conjunctiva and its neighbourhood are the afferent channels in the common reflex acts of winking and closing the eyelids; and the fibres from the nasal mucous membrane commonly excite the complexly co-ordinated involuntary act of sneezing.

3. *Excito-secretory.*—In the same way, as in the case of reflex motion, secretion is reflexly excited by the fibres which carry afferent impulses to the medulla from the anterior part of the tongue, when the latter is strongly stimulated, and thus excite activity of the salivary secretion; and severe stimulation of the mucous membrane of the nose or of the eye causes impulses to pass to the secretory centre of the lachrymal glands, which are frequently thus reflexly excited.

Very intense stimulation of almost any of the afferent nerves may excite these reflex phenomena. Thus the most stoic person will experience active secretions of saliva and lachrymal fluid, as well as spasmodic closure of the lids during the extraction of a tooth. Even the bold use of a blunt razor will cause the tears to flow down the cheeks, by sending excito-secretory impulses along the branches of the inferior and superior maxillary division of this nerve.

4. *Tactile impulses* are appreciated by the anterior part of the tongue with remarkable delicacy, and are conveyed by the lingual branch of the fifth nerve; and most of the cutaneous fibres are also capable of receiving tactile stimulation.

5. *Taste.*—The tastes that are appreciated by the anterior part and the edges of the tongue are carried by fibres which lie in the peripheral branches of this nerve. These, however, probably belong chiefly, if not altogether, to the chorda tympani, and leave this lingual branch of the fifth to join the seventh nerve on their way to the trunk of the glosso-pharyngeal.

There are four ganglia in close relation to the branches of the fifth nerve which have certain points of similarity, and may, therefore, be considered together, although their different positions show that they are engaged in the performance of very different functions.

We have not yet been able to ascertain the value of these little points of junction of motor, sensory, vaso-motor, and secretory fibres, because, so far, we are unable to attribute to the cells of the ganglia either reflecting or controlling action, or any automatic power.

They all have efferent (motor and secretory) and afferent (sensory) connections with the nervous centres, and also connections with the main channels of the sympathetic nerves. These are spoken of as the roots of the ganglia. Their little branches are generally mixed nerves.

The Ciliary or Ophthalmic Ganglion.

This ganglion lies in the orbit. It has three roots, which come from—(1) the inferior oblique branch of the third nerve, by a short slip, which forms the motor root; (2) from the nasal branch of the ophthalmic division of the fifth, and from the carotid plexus of the sympathetic. The branches go mostly to the ball of the eye, and may be divided into those which are afferent and efferent. The afferent are only sensory branches, connecting the cornea and its neighbouring conjunctiva with the centres. The efferent, or motor fibres, are those that go to the dilator pupillæ (coming mostly from the sympathetic), and the vaso-motor fibres going to the choroid coat, iris, and the retina.

The Sphenopalatine or Nasal Ganglion.

This lies on the second division of the fifth nerve, from which it gets its sensory root. Its motor root comes from the seventh by the great superficial petrosal nerve, and its sympathetic root from the carotid plexus by the branch joining this nerve. These enter the ganglion together, and are commonly spoken of as the vidian nerve. Afferent (sensory) impulses, from the greater part of the nasal cavity, pass through this ganglion. Its efferent branches are—(1) motor to the elevator of the soft palate and the azygos uvulæ; (2) vaso-motor, which come from the sympathetic; and (3) secretory, which supply the glands of the cheek, &c.

Otic or Ear Ganglion.

The otic ganglion lies under the foramen ovale, where the inferior division of the fifth comes out of the cranium. Its roots are—(1) motor; and (2) sensory, from the inferior division of the fifth; and (3) sympathetic, made up of a couple of fine filaments from the plexus, around the meningeal artery. By its branches it communicates with the seventh, chorda tympani, and sends filaments to the parotid gland.

THE SUBMAXILLARY GANGLION.

This is on the hyoglossus muscle in close relation to the lingual branch of the fifth, from which it gets a sensory root. The chorda tympani passes to the ganglion, carrying efferent impulses through it to the gland. Its sympathetic branches come from the plexus around the facial artery.

VIII.—THE GLOSSO-PHARYNGEAL NERVE.

This nerve forms part of the eighth pair, springs from the floor of the fourth ventricle above the nucleus of the vagus. It is a mixed nerve, the functions of which may thus be classified.

Afferent fibres, which are of various kinds, viz.:—

(1.) *Sensory fibres*, carrying impulses from the anterior surface of the epiglottis, the base of the tongue, the soft palate, the tonsils, the Eustachian tube and tympanum.

(2.) *Excito-motor*. This nerve is a very important exciter of reflex movements in swallowing and vomiting, when a stimulus is applied to the glosso-palatine arch.

(3.) *Excito-secretory*, the stimulation of the back of the tongue gives rise to a copious flow of saliva by means of reflex action.

(4.) *Taste* sensations are, for the most part, carried by this nerve; they are conveyed from special nerve-endings in the back of the tongue (see Taste).

The *efferent fibres* are not so varied, being simply *motor* to the middle constrictor of the pharynx, the stylo-pharyngeus, the elevator of the soft palate, and the azygos uvulæ.

THE SPINAL ACCESSORY NERVES.

These also form part of the eighth pair of nerves, and arise from the oblong and the spinal marrow, as low down as the seventh cervical vertebra. The lower fibres leave the lateral columns at their posterior aspect, and then run up between the denticulate ligament and the posterior roots of the spinal nerves to enter the cranial cavity. On their way out of the cranium they divide into two parts, one of which becomes amalgamated with the vagus, and the other passes down the side of the neck as the motor nerve of the sterno-mastoid and trapezius muscles. Physiologically, it may be compared with the anterior root of a spinal nerve, and the part accessory to the vagus most probably supplies that nerve with most of its motor branches.

THE VAGUS NERVE.

The vagus arises from the lower part of the floor of the fourth ventricle, and has connections with many of the important groups of nerve cells in this neighbourhood.

The functions of its widely-distributed fibres may be thus briefly stated :—

A. The EFFERENT FIBRES may be divided into—

1. *Motor-nerve* channels, going to a great portion of the alimentary tract and the air-passage ; the following muscles getting their motor supply from the branches of the vagus—the pharyngeal constrictors, some of the muscles of the palate, the œsophagus, the stomach, and the greater part of the small intestine. Motor impulses also pass along the trunk of the vagus—though leaving the cord by the roots of the accessory nerve—to the intrinsic muscles of the larynx ; these fibres lie in the inferior or recurrent laryngeal nerve except that to the crico-thyroid, which lies in the superior laryngeal branch. The tracheal muscle and the smooth muscle of the bronchial walls are also under the control of the pulmonary branches of the vagus.

2. *Vaso-motor fibres* are said to be supplied to the stomach and small intestine. These fibres are probably derived from some of the numerous connections with the sympathetic.

3. *Inhibitory impulses* of great importance for the regulation of the forces of the circulation pass along the vagus to the ganglia of the heart. As already explained in detail (see p. 224), these fibres are always acting, as shown by the fact that section of the vagi causes a considerable quickening of the heart-beat. On the other hand, if the distal end of the cut vagus be stimulated, the heart beats more slowly, and in some animals may come to a standstill in a condition of relaxation.

B. The AFFERENT FIBRES still more widely spread, are important for the functions of the various viscera. They are :—

1. *Sensory fibres* carry impulses from the pharynx, œsophagus, stomach, and intestine, and from the larynx, trachea, bronchi, and the lungs generally. The pneumonia which follows section of the

vagi depends on—(1) the removal of the sensibility, and the ease with which foreign matters can enter the air-passages; or (2) the violent breathing necessary when the motor nerves of the larynx are cut; or (3) the injury of trophic or vaso-motor fibres.

2. *Excito-motor nerves.* There is no nerve that can be compared with the vagus in the variety of the reflex phenomena in which it participates. Afferent fibres in this nerve cause spasm of the muscles of the thorax and govern the respiratory rhythm, and preside over the inhalation of the air and excite the expiratory muscles. Thus irritation of the mucous membrane at the root of the tongue, the folds of the epiglottis, larynx, trachea, or bronchi, causes spasmodic fits of coughing. Irritation of the pharyngeal or the gastric fibres gives rise, by reflex stimulation, to the act of vomiting.

Stimulation of the proximal cut end of the trunk of the vagus causes inspiratory effort and cessation of the breathing movements in the position of inspiration. Stimulation of the central cut end of the superior laryngeal branch, causes reflex spasm of the muscles of the larynx and a fixation of the expiratory muscles in the position of expiration. The fibres which regulate the respiratory rhythm consist of two sets, probably passing from the lungs to the inspiratory and expiratory centres, and causing each to act before its ordinary automatism would transmit any discharge of impulse to the thoracic muscles.

In the laryngeal branches are fibres which bear centrifugal impulses to the vaso-motor centres in the medulla, and excite the centres to action. These, which may be grouped with the excito-motor channels, are spoken of as "*pressor*" fibres, from the influence they exert upon the pressure of the blood in the arteries.

3. *Excito-inhibitory* fibres pass from the heart to the vaso-motor centre. Stimulation of these fibres, which take somewhat different courses in different animals, checks the tonic action of the vaso-motor centre, and greatly reduces the blood pressure. Hence these fibres form the *depressor nerve.* Its terminals in the heart are stimulated by distension of that organ; and the vaso-motor centre is thereby inhibited, the arteries dilate and the blood pressure falls so that the over-filled heart can empty itself.

4. *Excito-secretory fibres.* Stimulation of the gastric endings of the vagus causes not only gastric, but also the salivary secretion, which occurs as a precursor of gastric vomiting.

Section of both vagi in the neck causes the death of the animal within a day or two after the operation, and the following changes may be observed while it lives:—1. The heart-beat is much quicker as shown by the increased pulse-frequency. 2. The rate of breathing is very much slower. 3. Deglutition is difficult, the food easily passing into the air-passages through the insensitive larynx.

Section of the superior laryngeal nerves is followed by slight slowness of breathing, loss of sensibility in the larynx, entrance of food into the air-passages, chronic broncho-pneumonia, and death.

Section of the inferior laryngeal nerves gives rise to the same final result, because the muscles of the larynx are paralysed, and closure of the glottis is impossible. A change in voice follows the section or injury of even one inferior laryngeal, as may often be seen in man from the effect of the pressure of an aneurism.

IX.—Hypoglossal Nerve.

This nerve appears in the furrow between the olivary body and the anterior pyramid, on a line with the anterior roots of the spinal nerves. It corresponds with the anterior roots in function, being a purely motor nerve. It bears impulses to the muscles of the tongue and the other muscles attached to the hyoid bone.

Some sensory fibres lie in its descending branch, but these probably are derived from the vagus or trifacial nerves, with which its branches inosculate.

It is also said to contain the vaso-motor fibres of the tongue.

Section of the nerves causes paralysis of the muscles of the tongue; when this is unilateral, the tongue inclines to the injured side, while being protruded from the mouth; but while being drawn in, it passes to the sound side. This is easily understood when it is borne in mind that the two acts depend upon the intrinsic muscles of the tongue, bringing about an elongation or shortening of the organ respectively.

CHAPTER XXX.

SPECIAL SENSES.

It has been pointed out that the sensory nerves receive impressions from without and carry the impulse thus excited more or less directly to certain nerve cells in the brain where it becomes a sensation. The afferent nerves are, then, the means by which the mind becomes acquainted with occurrences in the outer world, as well as the channels along which a variety of stimuli pass to nerve centres whence they are reflected to different organs and parts, without causing any definite sensation in the nerve cells of the sensorium.

The ordinary sensory nerves are brought into such relationship to the surface that they are affected by slight mechanical stimuli, which throw the nerve fibres into activity, and send impulses to the brain. But we are capable of appreciating many other impressions besides mechanical stimulation. We can distinguish between degrees of heat and cold, when the difference is far too slight to act as a direct nerve stimulus. We can appreciate light, of which no degree of intensity is capable of exciting a nerve fibre to its active state, or of stimulating an ordinary nerve cell in the least degree. We recognise the delicate air-vibrations called sound, which would have no effect on an ordinary nerve ending. We can also distinguish several tastes; and finally, we are conscious of the presence of incomprehensibly small quantities of subtle odours floating in the air. When the amount of the substance is too small to be recognised even by spectrum analysis, which detects extraordinarily minute quantities, we can perceive an odour by our olfactory organs.

There must then be a special apparatus for the reception of each of these special impressions in order that the nervous system be accessible to such slender influences. In fact special mechanisms must exist by means of which heat, light, sound, tastes, and odour are enabled to act as nerve stimuli. These peculiar nerve terminals are known as the special sense organs, the physiology of which is one of the most difficult and most interesting branches of study in Biological Science.

The nerves which carry the impulses from the various organs of special sense do not differ from other nervous cords, so far as their structure and capabilities are concerned. But besides their special end organs they are connected with nerve cells in the brain, the sole duty of which is to receive impulses from one of the special sense organs and convert the same into a special sensation. No matter by what means a nerve trunk from a special sense organ be stimulated, the impulse excites in the sensorium the sensation usually arising from stimulation of the special organ to which it belongs. Thus electric stimulation of nerves in the tongue causes a certain taste; mechanical or other stimulation of the optic nerve-trunk gives rise to the sensation of flashes of light, and a persistent odour may be caused by the presence of a bony growth, pressing upon the olfactory nerve.

The capability of the nerve centres connected with the nerves of special sense to give rise invariably to a special sensation, is called their *specific energy*. And the special influence, light, sound, &c., which alone suffices to excite the special peripheral terminal, and which the given terminal alone can convert into a nerve stimulus, may be called its *specific* or *adequate stimulus*.

Although we habitually refer the sensation to the surface where the stimulus is applied, as if we really felt with our skin, and recognised sound sensations with our ears, &c., the sensation only occurs in the centres in the brain. This is obvious from what has been already said of the nerve-fibres of the special sense organs, namely, that if a stimulus be applied to the nerve trunk the same sensation is produced as if the specific stimulation had operated on the special nerve terminal from which these fibres habitually carried impressions. This peripheral localisation of sensations is really accomplished in the mind, just as by a mental act of a different character, the impressions communicated by the eye are projected into the space about us in our thoughts, instead of being referred to the retina, or thought of as being produced in the eye itself. This power of the centres of the sensorium to localise impressions to certain points of the skin, and to project into space the stimulation caused by the light reflected from distant objects, so as to get a distinct and accurate idea of their position, is the result of experience and habit, which teach each individual that when a certain sensation is produced, it means the stimulation of a certain point of the skin, and that the objects we see are not in our eyes, where the impulse starts, but at some distance from us. We learn this from a *long* series of unconscious experiments carried on in our early youth by movements of the eyes with co-operation of the hands. Even the sensations which arise in the various centres of the sensorium, as the result of internal or central excitations, are from habit attributed to external influences, and thus we have various hallucinations and delusions, such as seeing objects or hearing sounds which only exist in the brain.

The sensations produced in our nerve centres as the result of the afferent impulses coming from our special sense organs give rise to a form of knowledge called *perception;* each perception or impulse causing an appreciable sensation, helping to make up our knowledge of the outer world and of ourselves, for without this power of perception we could have no notion of our own existence and no ideas of our surroundings; in fact we should be cut off from all sources of knowledge and be idiots by deprivation of all intelligence from without.

A complete special sense apparatus may then be said to be made up of the following parts:—

1. A special nerve-ending only capable of being excited by a special *adequate stimulus.*
2. An afferent nerve to conduct the impulses from the special end-organ to the nerve-centre.
3. Nerve cells forming a centre, which is capable by specific energy of translating the nerve impulse into a *sensation*, and which sensation is commonly referred to some local point of the periphery.
4. Associated nerve centres, capable of *perceiving* the sensations, forming *notions* thereon, and drawing conclusions, from the present and past perceptions, as to the intensity, position, quality, &c., of the external influence.

SKIN SENSATIONS.

The sensations arising from the many impulses sent from the skin come under the head of special sense, and are commonly grouped together under the name of the *Sense of Touch.* This special sense may, however, be resolved into a number of specific sensations, each of which might be considered as a distinct kind of feeling, but usually are regarded as simply giving different qualities to the sensation excited by the skin. These sensations are:—(1) *Tactile Sensation*, or sensation proper, by means of which we appreciate a very gentle contact, and recognise the *locality* of stimulation, and judge of the position and form of bodies; (2) the sense of *pressure;* (3) and the sense of *temperature.*

The variety of perceptions derived from the cutaneous surface, and the large extent of surface capable of receiving impressions, make the skin the most indispensable of the special sense organs, though we value this source of our knowledge but little. If we could not place our hands as feelers on near objects to investigate their surfaces, &c., we should lose an important source of information that has contributed largely to our visual judgment. We think we know by the look of a thing what we originally learned by feeling it. If our conjunctivæ did not feel, we should miss its prompt warning, and our voluntary movements could not protect our eyes from many unseen injuries that normally never trouble us. If the skin were senseless it would require constant mental effort to hold a pen, and our power of standing and progressing would be most seriously impaired. And how utterly cut off from the outer world should we be, were we incapable of feeling heat and cold, the presence or absence of clothing, &c.

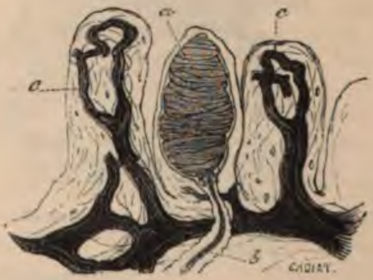


Fig. 208.—Drawing from a section of injected skin, showing three papillæ, the central one containing a tactile corpuscle (*a*), which is connected with a medullated nerve, and those at each side are occupied by vessels. (Cadiat.)

Nerve-Endings.

Although the end-organs of the nerves of the skin are the simplest of all those belonging to the apparatus of special sense, yet we have but a very imperfect knowledge of their immediate relationships to the different qualities or varieties of touch impressions. We are familiar with several different nerve-endings which are special terminals adapted for the reception of certain kinds of impressions, but what kinds of stimuli affect the different terminals we do not accurately know. They may be thus enumerated :—

1. The *Touch-corpuscles* (Meissner) are egg-shaped bodies situated in the papillæ of the true skin, underlying directly the epithelial cells of the rete mucosum. They occupy almost the entire papilla. The nerve fibres seem to be twisted around the corpuscle in a spiral manner, while the axis cylinders enter the body, and the covering of the nerve becomes amalgamated with its outer-wall. The touch-

corpuscles vary in size in different parts of the skin; usually being larger where the papillæ in which they lie are well-developed. The exact mode of ending of the axis cylinder is not satisfactorily understood.

2. *End-bulbs* (Krause) are smaller than the last and are less generally distributed over the surface of the body, being localised to certain parts. They are chiefly found in the conjunctiva and mucous membranes of the mouth and external generative organs. They consist of a little vesicle containing fluid in which the axis cylinder of a nerve terminates, the membrane which forms the vesicle of the bulb being fused with the sheath of the nerve. Many different shapes and varieties of these bodies have been described, but there seems to be no very definite morphological or physiological distinctions between the different varieties.

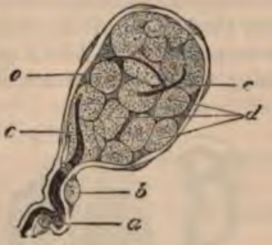


Fig. 209.—End bulb from human conjunctiva, treated with osmic acid, showing cells of core. (Longworth.)

a, Nerve fibre; *b*, nucleus of sheath; *c*, nerve fibre within core; *d*, cells of core.

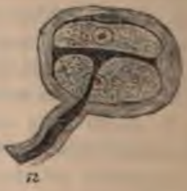


Fig. 210. — Tactile corpuscle from the duck's tongue, containing two tactile cells between which lies the tactile disc. (Izquierdo.)

3. *Touch-cells* (Merkel) are found in the deeper layers of the epidermis of man as well as in the tongues of birds, they are large cells with distinct nuclei and nucleoli. Frequently they are grouped together in masses and surrounded by a kind of sheath of connective tissue; in which condition they resemble touch-corpuscles.

4. *Free nerve-endings* occur on the surface of the epithelium of the mucous membranes, and are seen on the surface of the cornea. Here delicate, single strands of nerve fibrils can be seen after gold staining, passing between the epithelial cells and ending at the surface in very minute blunted points or knobs.

Naked nerve-fibrils have also been traced into the deeper layers of the epidermis of the skin, where they end among the soft cells of the mucous layer, either in branched cell-like bodies (Langerhaus), or delicate loops (Ranvier).

In the subcutaneous fat-tissue as well as in parts remote from the surface are large bodies, easily visible to the naked eye, commonly called—

5. *Pacinian corpuscles.* They are ovoid bodies made up of a great number of concentrically arranged layers of material, of varying consistence, with a collection of fluid in the centre in which an axis cylinder ends. There is no doubt that they are the terminals of afferent nerves, but if they belong to the sense of touch, which is doubtful, it is unknown to what special form of sensation they are devoted. From their comparatively remote relation to the skin, lying some distance beneath it and not in it, as are the other endings mentioned—they are probably connected with the appreciation of pressure sensations rather than those more properly called tactile.

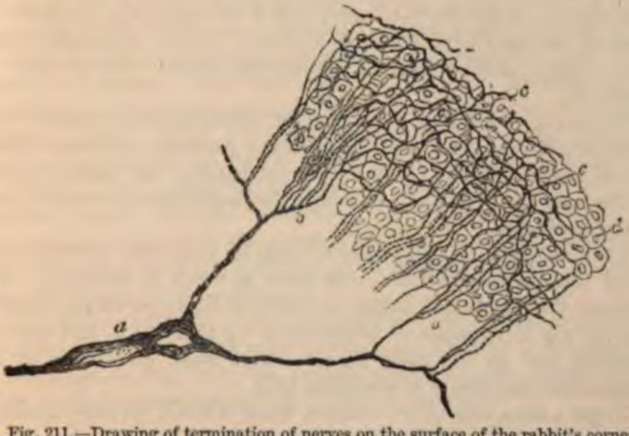


Fig. 211.—Drawing of termination of nerves on the surface of the rabbit's cornea. *a*, Nerve fibre of sub-epithelial network; *b*, Fine fibres entering epithelium; *c*, Intra-epithelial network. (Klein.)

The sense of touch must be carefully distinguished from ordinary sensibility or the capability of feeling pain, which is not a *special* but a *general* sensation, and is received and transmitted by different nerve channels. This we know from the facts, that the mucous passages in general can receive and transmit painful but not tactile *impressions*, and that in the spinal cord the sensory and tactile impulses pass along distinct tracts. Further, certain narcotic poisons destroy ordinary sensation without removing the sense of touch. This effect is also brought about by cold, when for instance the fingers are benumbed, gentle contact excites tactile impressions, while the ordinary sensations of pain can only be aroused with difficulty even by severe pressure.

However, most of the nerves we are in the habit of calling sensory nerves convey tactile impressions, and speaking generally the parts of the outer skin which have the keenest tactile sense are also the most ready to excite feelings of pain.

The intensity of the stimulation for the sense of touch must be kept within certain limits in order that it be *adequate*, *i.e.*, capable of exciting the specific mental perceptions. If the stimulus exceed these limits, only a general impression, namely that of pain, is produced.

The power of forming judgments by feeling an object differs very much in different parts of the body, being generally most keen where the surface is richest in touch corpuscles, namely, the palmar aspect of the hands and feet, and especially the finger-tips, the tongue, the lips, and the face.

When we feel a thing in order to learn its properties, we make use of all the qualities of which our sense of touch is made up. We estimate the number of points at which it impinges on our finger-tip, we rub it to judge of smoothness, we press it to find out its hardness, and at the same time we gain some knowledge of its temperature and power of absorbing heat.

To get a clear idea of our complex sense of touch we must consider each of the different kinds of impressions separately.

SENSE OF LOCALITY.

By this is meant our power of judging the exact position of any point or points of contact which may be applied to the skin. Thus if the point of a pin be gently laid on a sensitive part of the skin we know at once when we are touched, and if a second pin be applied in the same neighbourhood, we feel the two points of contact and can judge of their distance from one another and their relative position. When we feel a body we receive impulses from many points of contact bearing varied relationships to each other, and thus we become conscious of a rough or a smooth surface.

The delicacy of the sense of locality differs very much in different parts of the skin. It is most accurate in those parts which have been used as touch organs during the slow evolution of the animal kingdom.

The method of testing the delicacy of the sense of locality is simply to apply the two points of a compass to the different parts of the skin, and by varying their position, experimentally, determine the nearest distance at which the two points give rise to distinct sensations. The following precautions must be attended to in carrying out this experiment. 1. The points must be simultaneously applied or the two distinct sensations will be produced even at very close distances. 2. The force with which the points are applied must be equal and minimal, because excessive pressure causes a diffusion of the stimulus and a blurring of the tactile sense. 3. Commencing with greater and gradually reducing the distance of the points enables a person to appreciate a less separation than if the smaller distances were used at first. 4. The duration of the stimulus; two points of contact being distinguished at a much nearer distance if the points be allowed to rest on the part, than when they are only applied for a moment. 5. The temperature and material of the points should be the same. 6. Moisture of the surface makes it more sensitive. 7. Previous or neighbouring stimulation takes from the accuracy of the sensations produced. 8. The temperature of the different parts of the skin should be equal, as cold impairs its sensibility.

The following table gives approximately the nearest distances at which some parts, which may be taken as examples of the most and least sensitive regions of the skin, can recognize the points of contact by their giving rise to two distinct sensations :—

Tip of the tongue	1 mm.
Palmar aspect of the middle finger-tip	2 „
Tip of the nose	4 „
Back of the hand	15 „
Plantar surface of great toe	18 „
Fore arm, anterior surface	40 „
Front of thigh	55 „
Over ensiform cartilage	50 „
Between scapulæ	70 „

If one point of the compass be applied to the same spot, and the other moved around so as to mark out in different directions the limit at which the points can be distinguished as separate, we get an area of a somewhat circular form, for which the name sensory circle has been proposed. It would be very convenient to explain this on the simple anatomical basis that the impressions of this area were carried by one nerve-fibre to the brain, and thus but the one sensation could be produced in the sensorium. But we know this cannot be the true explanation, because of the following facts. 1. No such anatomical relationship is known to exist. 2. By practice we can reduce the area of our sensory circles in a manner that could not be explained by the development of new nerve-fibres. 3. If the two points of the compass be placed near the edges of two well-determined neighbouring sensory circles, and so in relation with the terminals of two nerve-fibres, they will not give distinct impressions; in fact they require to be separated just as far as if they were applied within the boundary of one of the circles where they also give rise to the double perception.

To explain better the sense of locality it has been supposed that sensory circles are made up of numerous small areas, forming a fine mosaic of *touch-fields*, each of which is supplied by one nerve-fibre, and that a certain number of these little fields must intervene between the stimulating points of the compasses in order that the *sensorium* be able to recognize the two impulses as distinct. For, although every touch-field is supplied by a separate nerve-fibril which carries its impulses to the brain, and is therefore quite sensitive, the arrangements in the sensorium are such that the stimuli carried from two adjoining touch-fields are confused into one sensation. Thus, when an edge is placed on our skin, we do not feel a series of points corresponding to the individual fields with which it comes in contact, but the confusion of the stimuli gives rise to an uninterrupted sensation, and we have a right perception of the object touched.

THE SENSE OF PRESSURE.

There seems to be a reason for separating the perception of differences in the degree of pressure exercised by a body from the simple tactile or local impression. If we support a part of the body so that no muscular effort be called into play in the support of an increasing series of weights placed upon the same area of skin, we can distinguish tolerably accurately between the different weights. It has been found that if a weight of about 30 grammes be placed on the skin a difference of about 1 gramme can be recognized—that is, we can distinguish between 29 and 30 grammes, if they are applied soon after one another. If the weights employed are smaller, a less difference can be detected; if larger weights are used the difference must be greater, and it appears that the weight-difference always bears the same proportion to the absolute weight used. We can perceive a difference between 7¼ and 7½, 14½ and 15, 29 and 30, 58 and 60, &c., the discriminating power decreasing in proportion as the absolute degree of stimulation increases.

One of the reasons why the sense of locality is regarded as distinct from that of pressure is that the latter is found not to be most keenly developed in the same parts where the impressions of locality are most acute. Thus judgment of pressure can be more accurately made with the skin of the fore-arm than the finger-tip, which is nine times more sensitive than the former to ordinary tactile impressions, and the skin of the abdomen has an accurate sense of pressure though deficient in ordinary tactile sensation.

It has been said above that the weights by which pressure-sense is to be tested should be applied rapidly one after the other. This fact depends upon the share taken in the mental judgment by the function we call memory. In a short time the recollection of the impression passes away and there no longer exists any sensation with which the new stimulation can be compared.

At best we can form but imperfect judgments of pressure by the skin impressions alone. When we want to judge the weight of a body we poise it in the free hand, which is moved up and down so as to bring the muscles which elevate it into repeated action. Hereby we call into action a totally different evidence, namely, the amount of muscle power required to raise the weight in question, and we find we can arrive at much more accurate conclusions by this means. The peculiar recognition of how much muscular effort is expended is commonly spoken of as *muscle-sense*, which may arise from a knowledge of how much voluntary impulse is expended in exciting the muscles to action, but more probably it depends upon afferent impulses arriving at the sensorium from the muscles. By its means we aid the pressure-sense in arriving at accurate conclusions of the weight of bodies, so that in the free hand we can distinguish between 39 grm. and 40 grm.

TEMPERATURE SENSE.

We are able to judge of the differences in temperature of bodies which come in contact with our skin. Since our sensations have no accurate standard for comparison we are unable to form any exact conception of the absolute temperature of the substances we feel. The sensation of heat or cold, derived from the skin itself, with-

3. ARTHR
with in the
lining the
which cover
and form wh
is strengthene
ment—which
the periosteum,

The articula
pressed togeth
and tonic contr
siderable tracti
ligaments, whi
matter what th
in the knee-joi
ligaments suffic
atmospheric pr
tion, as may be
lated, even wh
have been sever

The synovial
their surfaces, or

1. Flat articul
allowing of but
of joint are to be
the vertebræ.

2. Hinge joint
kind of motion
fits closely and
while the sides
strong lateral lig
found between th
joint.

3. The rotatory
moves round th
being at right ang
nary hinge. Such
at the articulatio
the axis.

4. A saddle-sha
of the two articula
hence there are tw

These nerve endings are not the same as those that receive touch d pressure impressions, because the appreciation of temperature fferences is not most delicately developed in the parts where the ctile sensations are most acute. Thus the cheeks and the eyelids e especially sensitive to changes of temperature, a fact known by ople who want a ready gauge of the heat of a body—thus a barber proaches the curling-tongs to his cheek to measure its temperature fore applying it to the hair of his client. The middle of the chest, oreover, is very sensitive to heat, while it is dull in feeling tactile npressions.

The hand is far from being the best gauge of temperature, for eat appreciation is not developed in a due proportion to the keeness of the tactile sensibility. The larger the surface exposed to hanges of temperature the more accurate the judgment at which e can arrive — the slightest changes being at once recognized hen the entire surface of the body is exposed to them. The foreoing facts are well known to persons in the habit of testing the mperature of a warm bath without the aid of a thermometer; hey do not use the limited surface of a sensitive tactile finger-tip ut plunge the entire arm into the water. The elbow, indeed, is the ommon test used by nurses in ascertaining that the water in which hey are about to wash an infant is not too warm for that purpose.

Great extremes of heat or cold, such in fact as would act as stiuli to a nerve fibre, do not give rise to sensations of different mperatures, but simply excite feelings of pain. Thus, if one lunges one's hand into a freezing mixture or into extremely hot ater, it is difficult to say at once whether they are hot or cold—in oth cases pain being the only sensation produced.

GENERAL SENSATIONS.

We call general sensations those feelings, pleasurable or otherwise, which can be excited in us, without our being able to refer them to xternal objects, or compare their sensation with those of the special enses, or even to describe their exact mode of perception. Under his head are enumerated Pain, Hunger, Thirst, Nausea, Giddiness, Shivering, Titillation, Fatigue, &c.

Of these only *pain* is commonly referred to any given part, and he attempt to localize pain with exactness soon shows how very ifferent is our power in this respect in the case of pain and in the case f tactile *impressions*. Thus when we strike our "funny-bone" (the *ulnar nerve passing* over the condyle of the humerus), by the tactile impressions of the skin we know the elbow is the injured part, but the locality of the pain is not so exactly to be determined, for it shoots down the arm to the little finger, and is indefinitely spread over the region to which the nerve is distributed.

In studying the laws which govern the perception of painful impressions we must make the experiments upon ourselves, since we alone can form conclusions from the sensations produced.

The best way to carry out experiments upon pain is to use extremes of temperature, as we can thus graduate the stimulation. The application of a liquid over 50° C., or below 2° C., causes pain. The suddenness of application to the part, and its duration, and the extent of surface, as well as the previous temperature, have important influence in the amount of pain produced.

The various kinds of pain which we are all more or less familiar with seem to be related in some way to their mode of production, but we are unable to assign any definite cause for these differences of character. Thus, though such terms as shooting, stabbing, burning, throbbing, boring, racking, dragging pain, have a tolerably clear meaning in general, and may be of diagnostic value, we have only an indistinct knowledge that throbbing depends on excessive vascular distention in a part, that sharp pains are produced by sudden excitation of a sensitive part, and that the dull pains by the more permanent stimulation of a part less well supplied with nerves.

Further, pain as we think of it is a complex mental process, made up of many items, such as real sensory impressions, fear, disgust, &c. When a finger is being lanced patients often cry out most loudly before they are touched with the knife, and show intense feeling when they look at the blood flowing from the wound.

Hunger and *thirst* are peculiar and indefinite sensations which are experienced when some time has elapsed since food or drink has been taken. The exact part of the nervous system in which these impressions arise has not been determined. They are, however, said to be associated with peculiar sensations in the stomach and throat respectively. In the same way the venereal appetite, though associated with local sensations, cannot be referred to any one part of the nervous system.

Nausea is also a sensation which cannot be attributed to any part of the nervous centres. It commonly arises in response to afferent impulses, such as smells, sights, tastes, pharyngeal, gastric, or other visceral irritation, and is antagonistic to the appetites just named. All the sensations that give rise to or precede nausea are associated in our minds with disagreeable impressions, and no doubt mental operations have much to do with its production. A child, free from affectation, may be heard to say of a castor-oil bottle which in itself is not ugly, "I can't bear to look at it, the very thought of it makes me feel sick."

However, even without any participation of the mental functions, unavoidable nausea may come on from irregular motion, as that of a ship, which often causes nausea in those unaccustomed to the sea. Certain conditions of the blood flowing through the nerve centres also cause nausea, as when emetics are injected into the blood.

Giddiness, which consists in a feeling of inability to keep the normal balance, is often produced in connection with the last by irregular movements, but more surely by a rotatory motion of the body. Other afferent influences may give rise to it, viz., from the stomach, in some cases of irritation; from the eye, when we look from a height; from the semicircular canals of the ear by rotation of the body; and also from conditions of the blood, as in alcoholic toxæmia.

Shivering is also the result of a peculiar nervous effect produced by afferent influences of an unpleasant kind, the sudden application of cold to the skin, a revolting sight, a shrill noise, an intensely nasty taste, and a very shocking narrative, may excite a nervous condition which makes us shiver.

Titillation follows light stimulation of certain parts of the cutaneous surfaces. It is a peculiar general sensation, in moderation not disagreeable, and usually accompanied by a tendency to meaningless laughter or reflex movements.

CHAPTER XXXI.

TASTE AND SMELL.

SENSE OF TASTE.

NEXT to the sense of touch, which is distributed more or less over the whole cutaneous surface, taste is the least localised anatomically. Though confined to the cavity of the mouth, its more accurate limitations are not easily fixed. The point, sides, and posterior part of the dorsum of the tongue can most accurately appreciate tastes; and probably parts of the palate also have the power, but in a much less degree. Indeed, though "the palate" is often spoken of as if it were the seat of taste, it really enjoys this function in an insignificant degree when compared with the tongue.

The power of being stimulated by various tastes is not restricted to the terminals of any one nerve, but is shared by some of those of at least three trunks, which also transmit impulses arising from other forms of stimulation. The glosso-pharyngeal division of the 8th pair sends branches to the posterior part of the tongue, which are no doubt connected with the special taste organs. The lingual branches of the 5th—commonly called the gustatory nerves—have also terminals capable of being excited by taste, and probably some fibres of the chorda tympani are also employed in this function.

In the furrows around the circumvallate papillæ, and also, but more sparsely, on the sides of the fungiform papillæ of the tongue, are found peculiar organs called "taste-buds" or "taste-goblets." They are embedded in the stratified epithelium, with the cells of which their outer layers are intimately connected. They are flask-shaped bodies, composed of a concentric series of flattened cells pinched together at the base and at the free surface, where they seem to enclose a kind of orifice. Near the centre the flattened scales are replaced by short thread-like elements, so that the whole reminds one somewhat of the construction of the head of an artichoke.

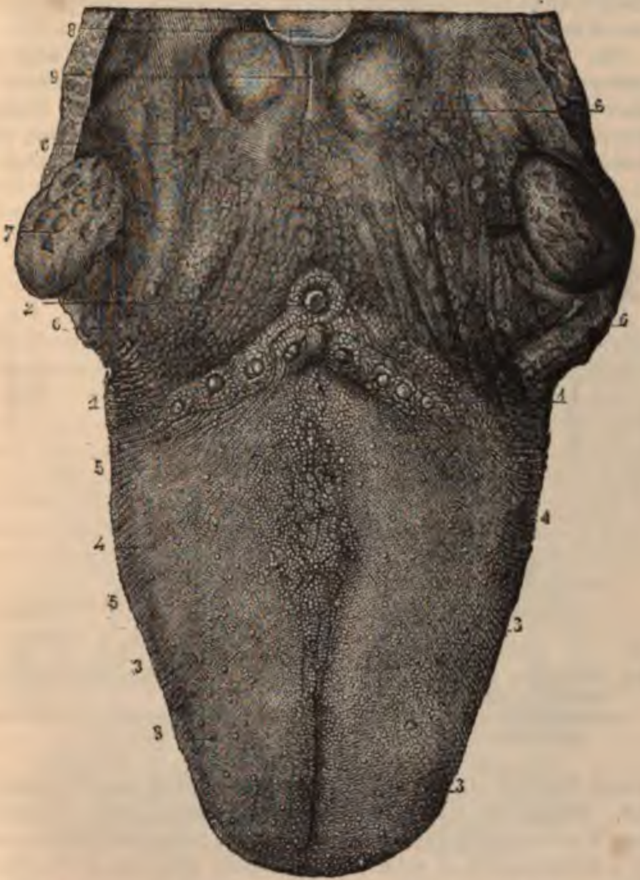


Fig. 212.—Drawing of upper surface of the tongue, showing the position of the circumvallate papillæ (1). (Sappey.)

Nerves can be seen entering these bodies, and are in all probability directly connected with the modified epithelial cells of which they are made up. The relation of the glosso-pharyngeal nerves to these taste-buds has been shown by the fact that in the rabbit (in which *animal they* are crowded together in a special organ so as to be easily found) they degenerate, and in a few months disappear, after one of these nerves has been cut.

The genuine taste sensations are very few. Much of what we commonly call taste depends almost exclusively upon the smell of the substance, and we habitually confuse the impressions derived from these two senses.* The different tastes have been divided into four, viz., sweet, sour, bitter, and salt, under some one or other of which headings all our tastes, properly so called, would naturally fall. Though this classification has no just claim to being a chemical one, it is interesting to know that each taste pretty well corresponds to a distinct group of substances chemically allied one to the other. Thus, acids are sour, alkaloids are bitter, the soluble neutral salts of the alkalis are salt, and polyatomic alcohols, as glycerine, grape sugar, &c., are commonly sweet.

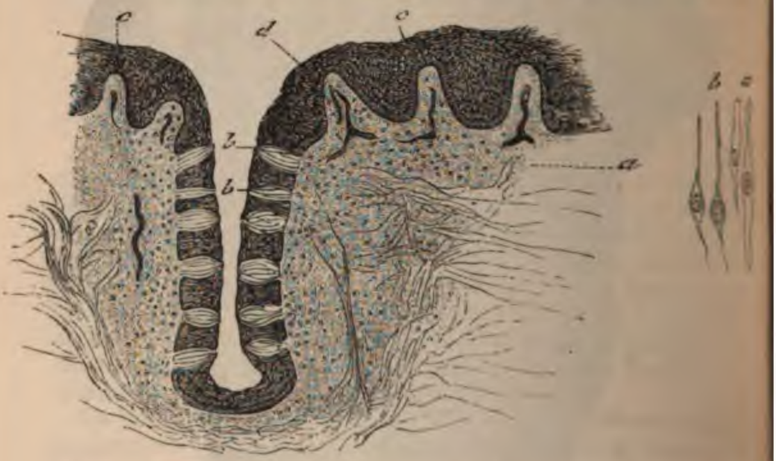


Fig. 213.—Section through depression between two circumvallate papillæ, showing taste-buds. (Cadiat.)
a, fibrous tissue of papilla; *d* and *c*, epithelial covering of papilla; *b*, taste-buds. On the right *a*, *b*, show the separate cells of a taste-bud.

The substances most probably act on the nerve terminals as chemical stimuli, because they must be in solution to be appreciated. If solid particles be placed on the tongue they must be dissolved in the mouth fluid before they can excite the taste organs.

---

* Many of the comestibles, the taste of which we most prize, have really no taste, but only a smell which we habitually confound with taste, having mingled the experience obtained from the two senses. Thus, if the draft of air be carefully excluded from the nose, wine, onion, &c., may easily be proved to have no taste. Hence the familiar rule of holding the nose adopted in taking "bad-tasting" medicine.

In order to explain the appreciation of the different tastes we may imagine that there are different kinds of terminals, each of which is or is not influenced by various substances according as they possess a special sweet, sour, bitter, or salt energy. From these different terminals pass fibres bearing impulses to certain central cells, each of which is capable of exciting a sweet, sour, bitter, or salt sensation, as the case may be.

SENSE OF SMELL.

The numerous delicate nerves which pass from the olfactory bulb to the mucous membrane of the upper and part of the middle meatus of the nose form the special nerves of smell. When certain subtle particles we call odours come in contact with the terminals of these nerves they excite impulses which, on arriving in the special centres of the brain, give rise to the impressions of smell.

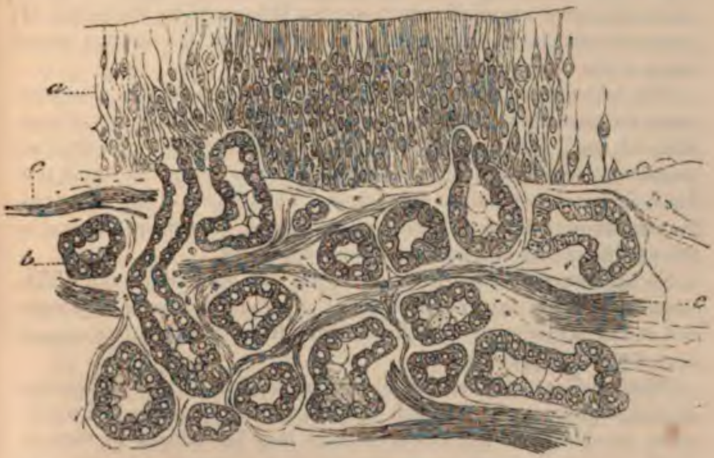


Fig. 214.—Section through the mucous membrane of the nasal fossa in the level of the olfactive region.
a, Epithelial cells and bundles of nerves; *b*, Glands separated from each other by bundles of nerves, *c*. (Cadiat.)

Anatomically the relations of the olfactory region are well defined. Its mucous membrane is not covered with motile cilia, as is that of the rest of the nasal cavity, and it is less vascular and peculiarly pigmented, looking yellow to the naked eye when compared with the neighbouring membrane. The epithelial cells are elongated into peculiar cylinders, between which lie long thin rods, ending on the surface in free hair-like processes. The deeper extremities of these rod-shaped filaments expand to surround a nucleus, and are then continued into a network of filaments, into which prolongations of the epithelial cells also seem to pass, and in which the delicate fibrils of the olfactory nerve can be traced. The existence of direct communication between the nerves and the rod-shaped filaments and the epithelial cells is satisfactorily established.

The odorous particles must be in the form of gases, in order to be carried by the air into the olfactory region, and the air must be kept in motion, by sniffing it in and out of the nasal cavity, in order to excite the nerve terminals, which are not influenced by the odours of air absolutely at rest, though it be in contact with the mucous membrane of the olfactory tract.

The extreme delicacy of appreciation of odours by the olfactory nerve terminals is very remarkable. Even in human beings, whose sense of smell is but poorly developed when compared with that of animals, an amount of odorous substance can be perceived which the finest chemical tests fail to appreciate. Thus Valentin has estimated that the two-millionth of a milligram of musk is sufficient to excite the specific energy of a man's olfactory apparatus.

No satisfactory classification of odours has been made out. The common division into agreeable and disagreeable smells, or scents and stinks, is dissimilar in different individuals, and therefore cannot have a physiological basis.

With smell, as with taste, no degree of intensity of stimulation can be said to produce pain, though disgust, nausea, vomiting, and many other psychical and nervous operations may be induced by various smells, and the appetites are either excited or annulled by different excitations of the olfactory nerves.

CHAPTER XXXII.

VISION.

NEXT in importance to the intelligence we receive from the skin is that which is conveyed to the brain from the outer world by the second pair of cranial, or the optic nerves.

The ending of the optic nerve differs from any of those we met with in the skin, by being enclosed in a very specially arranged organ —the eyeball—an apparatus for bending the rays of light, so that they exactly reach the delicate sheet of complicated nerve-ending which is here spread out. Nothing but the blood and other tissues of the eye come in contact with the endings of the optic nerve, which is thus placed out of the way of ordinary nerve stimulation. Indeed, we shall see that the light, of which the optic nerves convey intelligence to the brain, is not properly a nerve stimulus, being merely the waving of an imponderable medium, the existence of which is assumed. Besides the special arrangements in the eyeball for bringing the rays of light to bear on the nerve-endings, there must here be some extremely delicate arrangement by which the ether-waves, that we call light, can be converted into a nerve stimulus, or in some way made to affect the nerve terminals in the retina.

By means of the sense of sight we obtain knowledge of objects at a distance from us, because all these objects reflect more or less light, and thus make different impressions upon the terminals of the optic nerve, which form the outer layer of the retina.

Light, then, is the *adequate stimulus* for the retinal nerve-endings, and the impulse caused by light is the only impression the optic nerve is in the habit of carrying to our sensoria, where the sensation of light is formed and distributed among the cells of the brain so as to enable us to come to visual conclusions and judgments. As already mentioned, no matter what stimulus electric, mechanical, or other, be applied to the fibres of the optic nerve, the sensation produced is simply light, and this is thought of as if it came through the eye from the outer world.

The study of sight may then be divided into :

1. The path the light takes on its way through the eye to reach the retina.

2. The molecular changes in the retina which give rise to stimulation of the optic nerves.

3. The sensations arising in the sensorium as the result of the molecular changes set up in the cerebral nerve cells by the impulses from the optic nerve.

4. The visual perceptions and judgments which our consciousness is capable of elaborating from the visual sensations.

THE TUNICS OF THE EYEBALL.

The organ of vision of vertebrate animals is enclosed in a firm case of fibrous tissue called the *sclerotic coat*, which is continuous with the sheath of the optic nerve, and is seen between the eyelids under the transparent conjunctiva, and is commonly known as the white of the eye. It gives shape and protection to the eye, and though translucent, is not transparent. In front a round window-like portion, called the *cornea*, forms the most anterior segment of this protecting covering of the eyeball. The cornea is distinguished from the sclerotic not only by its glass-like transparency, but also by being part of a lesser sphere than the sclerotic, and thus it projects a little more than the rest of the bulb.

Closely attached to the inside surface of the sclerotic is a soft, thin, black vascular sheet of tissue which supplies the eyeball with blood, being made up chiefly of blood-vessels and stellate, pigmented, connective tissue cells. Its outer layer is traversed by arteries and veins of relatively large size, and its inner layer is practically composed of a dense network of close-meshed capillary vessels. As the cornea is approached, the choroid is peculiarly modified and thrown into folds, called *ciliary processes*, forming a series of vascular projections, which radiate from the margin of the cornea. At the edge of the cornea the choroid is more firmly attached to the sclerotic by a circular muscle (*the ciliary muscle*), and also by bands of tissue from the posterior surface of the cornea which hold it in position; the fibres of the ciliary muscle, running under the ciliary processes, radiate from the margin of the cornea towards the choroid, to which they are attached. In a modified form, known as the *iris*, this vascular and pigmented coat of the eye leaves the sclerotic, and hangs freely in a fluid so as to be recognised through the clear cornea as a coloured circular curtain, attached to the inside of the periphery of the cornea, and having a central deficiency, which looks black, and is familiarly known as the *pupil.* The pupil is merely an opening in the iris, which allows the rays of light to pass into the interior of the eyeball.

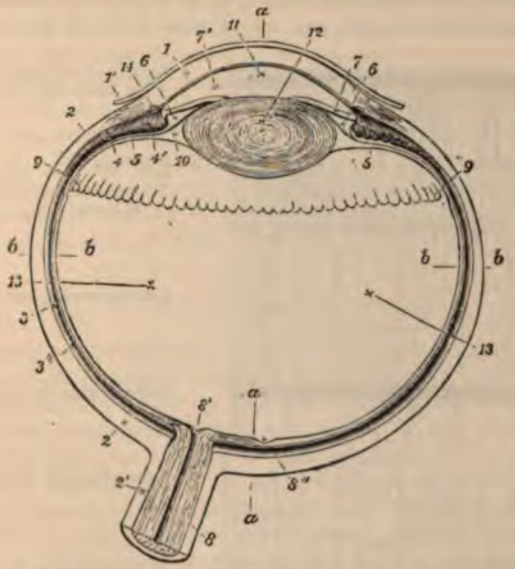


Fig. 215.—Diagram of a horizontal section through the human eye.

1. Cornea; 2. Sclerotic; 3. Choroid; 4. Ciliary processes; 5. Suspensory ligament of lens; 6. So-called posterior chamber, between the iris and the lens; 7. Iris; 8. Optic nerve; 8'. Entrance of central artery of the retina; 8''. Central depression of retina or yellow spot; 9. Anterior limit of the retina; 10. Hyaloid membrane; 11. Aqueous chamber; 12. Crystalline lens; 13. Vitreous humour; 14. Circular venous sinus which lies around the cornea; a—a, antero-posterior, and, b—b, transverse axis of bulb.

Besides supplying nutrition to the non-vascular central parts of the eyeball, the choroid is useful in vision by preventing the reflection of the light from the background of the eye in such a way as would cause irregularity of its distribution, and thus dazzle and interfere with the distinctness of the image. The choroid also is elastic, and can move over the neighbouring sclerotic; it can be drawn forwards by the contraction of the radiating ciliary muscle, which acts as a tensor of the choroid membrane.

The iris has a special power of motion, by means of which the opening in it can be made smaller, so as to regulate the amount of light admitted to the eye, and cut off more or less of the rays which would pass through the margin of the dioptric media. The importance of this will be better understood further on.

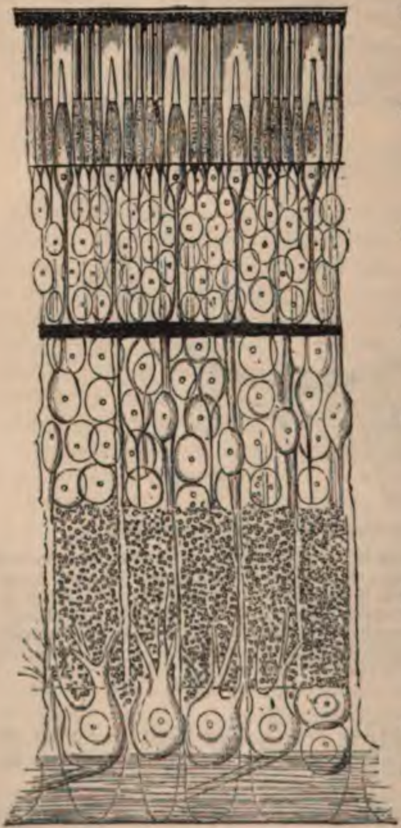

Pigmented epithelium lying next to the choroid coat.
Rods and cones with their extremities embedded in the epithelial cells.
External nuclear layer.
External granular layer.
Internal nuclear layer.
Internal granular layer.
Layer of nerve cells.
Nerve fibre layer in which the retinal vessels run next to the vitreous humour.

Fig. 216.—Diagrammatic section of retina showing the relation of the different layers in the posterior part of the fundus (not the *macula lutea*). (Schultze.)

Within the choroid coat, and in immediate contact with it, is the nervous coat, or *retina,* formed by the expansion of the optic nerve, which pierces the sclerotic a little obliquely, entering it somewhat to the nasal side of the axis of the eye. The retina lines all the back part of the eyeball, and stretching forwards, becomes fused with the ciliary processes, where, however, the nervous elements of the coat are wanting. The fibrils of the optic nerve reach the inner surface of the coats of the eye, and lie in immediate relation to the transparent medium, which occupies the greater part of the bulb. The fibres then lie internally to their terminals, which turn outwards and are set against the choroid coat. The ultimate nerve-endings are situated in pigmented protoplasmic cells, which form the outermost layer of the retina.

THE DIOPTRIC MEDIA OF THE EYE-BALL.

The transparent substances which fill the eyeball are, together with the cornea, commonly called the dioptric media. The *aqueous humour* lies in contact with the posterior surface of the cornea, and just fills the prominence which is formed by this part of the eye. It is in this fluid that the movable iris is stretched and separates the aqueous department of the eye into an interior and posterior chamber. The *vitreous humour* occupies much the larger share of the eyeball. It lies in apposition to the retina, being separated from it only by a thin transparent structure, called the *hyaloid membrane,* which encloses the clear gelatinous vitreous humour, and is fused with the ciliary part of the retina and choroid. The vitreous humour is developed from the young connective tissue of the mesoblast, and we find in the adult that mucus is the most striking chemical substance in its texture, though the form elements of the original mucous tissue have nearly all disappeared.

The most important of the dioptric media is the *crystalline lens.* It is placed between the aqueous and the vitreous humours, just behind the iris, which lies in contact with its anterior surface. It is like a strong magnifying glass, bi-convex in shape, the posterior surface being more convex than the anterior. The lens is much harder than the vitreous humour, but its outer layers are but little denser than a stiff jelly. It is enclosed by a firm elastic capsule, which is drawn tightly over the anterior surface, and influences its shape. The lens is held in its position by a thickened part of the soft, elastic hyaloid membrane, called the *suspensory ligament,* which is attached to the anterior surface of the capsule, near its margin. The lens and its capsule, together with the vitreous humour, may be said to be enclosed in the hyaloid membrane, which is thickened and fixed to the capsule, and to the ciliary part of the choroid. Thus any tension exercised by the suspensory ligament tends to tighten the anterior part of the capsule, and flatten the anterior surface of the lens.

The shape of the lens varies at different times of life, being nearly spherical in the infant and tending to become less convex in old age

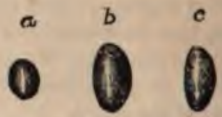


Fig. 217.—Diagram of lens at different periods of life.
a, At birth; *b*, Adult; *c*, Old age. (Allen Thomson.)

(v. fig. 217). The lens is developed from the outer layer of the embryo by the gradual thickening and growing inwards of the

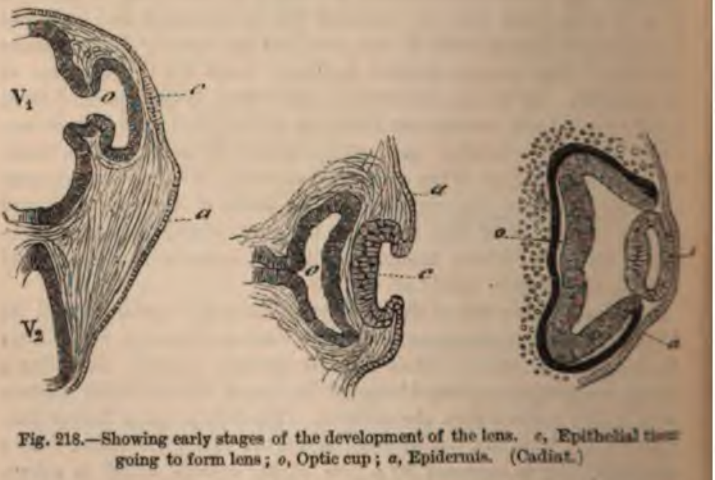


Fig. 218.—Showing early stages of the development of the lens. *e*, Epithelial tissue going to form lens; *o*, Optic cup; *a*, Epidermis. (Cadiat.)

epithelium, which meets the optic cup, and after a time is cut off from the parent tissue. The stages of its development may be followed in the accompanying woodcuts (v. fig. 218).

The lens is composed of a number of peculiar band-like cells, derived from the epithelium. These are cemented together in parallel rows, eccentrically arranged in layers. These bands are hexagonal in transverse section, and in the younger periods of life may be seen to contain nuclei.

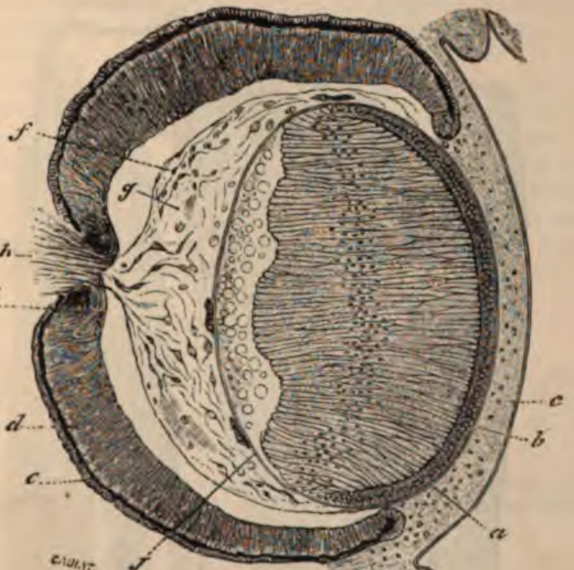


Fig. 219.—A further stage of the development of the lens. (Cadiat.)

a, Elongating epithelial cells forming lens; *b*, Capsule; *c*, Cutaneous tissue becoming conjunctiva; *d*, *e*, Two layers of optic cup forming retina; *f*, Cell of mucous tissue of the vitreous humour; *g*, Intercellular substance; *h*, Developing optic nerve.

In the living state the lens is perfectly transparent, but after death it becomes slightly opaque. The nutriment for the adult lens is derived from the vessels of the choroid, which, however, do not come into direct communication with its texture. On this account the nutrition of the lens is not so perfect as that of many other tissues, and it is but imperfectly repaired after injury, which always leaves more or less opacity. Even without injury, opacity, giving rise to cataract, sometimes occurs during life.

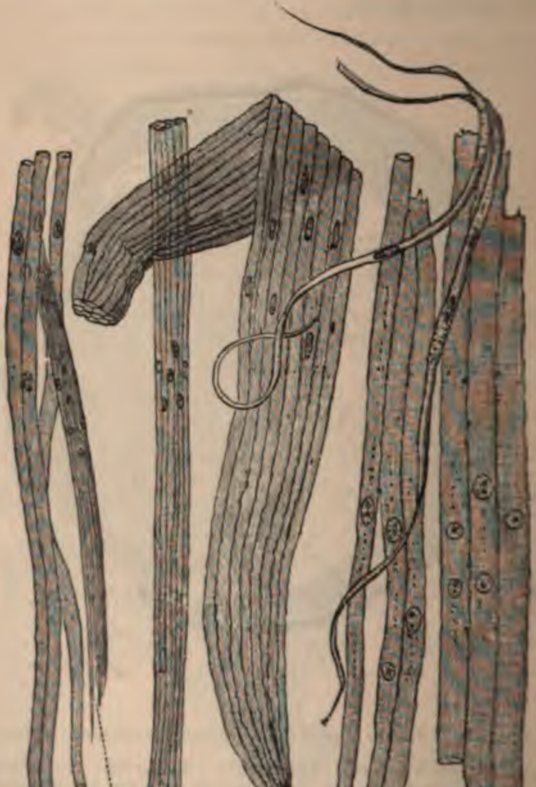


Fig. 220.—Fragment of lens teazed out to show the separate fibres. (Cadiat.) a, b, and c, show fibres with different sized nuclei.

Chemically the lens is made up of globulin, and furnishes a ready source for obtaining this form of albumin for examination.

THE DIOPTRICS OF THE EYE.

Light travels through any even transparent body, such as the atmosphere, in a straight line. But when it meets any change in density, particularly when it has to pass obliquely into a denser medium, the ray is bent so as to run in a direction more perpendicular to the surface of the denser body. The degree of bending or *refraction* of the rays depends chiefly on the difference in density of the two media and the angle at which the ray strikes the surface of the more dense.

On its way to the sensitive retina, the light has to pass through the various transparent media just named, viz., the cornea, the aqueous humour, the crystalline lens, and the vitreous humour. On entering these media, which have different densities, the rays of light reflected from any luminous body become bent or refracted, so that they are brought to a focus on the retina, just in the same way as parallel rays of light from the sun may be focussed on a near object by means of an ordinary convex lens.

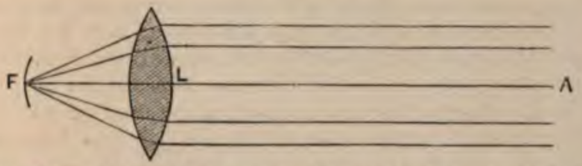


Fig. 221.—Diagram showing the course of parallel rays of light from A, in their passage through a biconvex lens L, in which they are so refracted as to bend towards and come to a focus at a point F.

Only so much light reaches the fundus of the eye as can pass through the opening in the iris, so that a comparatively narrow and varying beam is admitted to the chamber in which the nerve-endings are spread out for its reception.

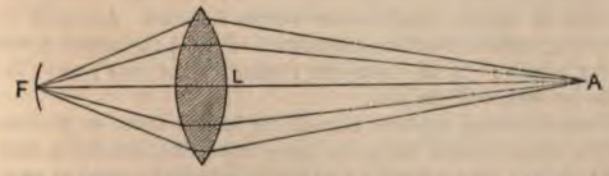


Fig. 222.—Diagram showing the course of diverging rays, which are bent to a point further from the lens than the parallel rays in last fig.

If we hold a biconvex lens at a certain distance from the eye and look out of the window through it, we see an inverted image of the landscape. If we place a piece of transparent paper behind the lens, we can throw a representation of the picture on it, which, however, will be seen to be inverted. This power of convex lenses is employed in the instrument used for taking photographic pictures, called a *camera*, which consists of a box or chamber into which the light is allowed to pass through a convex lens, so that an inverted image of the objects before it is thrown upon a screen of ground glass within the box. When the sensitive plate replaces the screen, the light coming through the lens makes the photographic picture.

Just in the same way an inverted image of the things we look at is thrown on the retina of the eye by the refracting media. This may be seen in a dark room, if a candle be placed at a suitable distance in front of the cornea of a fresh eye taken from a recently-killed white rabbit. When cleared of fat and other opaque tissues, the sclerotic is transparent enough to act as a screen upon which the inverted candle flame can be recognised.

Though our organ of vision is commonly compared to a *camera obscura*, the refractions of the light which occur in it are far more complex than those taking place in that simple instrument. In the latter we have only two media—the glass lens and the air; in the eye, on the other hand, we have several, which are known to have a distinct refractive influence on the rays which pass through the pupil.

Since the surfaces of the cornea, however, are practically parallel, we may neglect the difference between it and the aqueous humour, and look upon the two as one medium, having in front the shape of the anterior surface of the cornea, and behind, the anterior surface of the lens, so as to form a concavo-convex lens. We thus have only three media to consider, viz.: (1) the aqueous humour and cornea; (2) the lens and its capsule; and (3) the vitreous humour. And only three refracting surfaces need be enumerated, viz.: (1) the anterior surface of the cornea; (2) the anterior surface of the lens; and (3) the posterior surface of the lens.

These refracting surfaces may all be looked upon as portions of spheres whose centres lie in the same right line, and hence may be said to have a common axis. And the eye may be regarded as an optic system, centred around an axis which passes through the middle point of the cornea in front, and the central depression (fovea centralis) of the retina behind. This is commonly spoken of as the optic axis of the eye.

The rays of light entering the eye are most strongly refracted at the surface of the cornea, because they have to pass from the rare medium, the air, to the denser cornea and aqueous humour. So also more bending of the rays occurs between the aqueous humour and the anterior surface of the lens than between the posterior surface of the lens and the vitreous humour.

The lens is not of the same density throughout, but denser in the centre, and being made up of layers, the central part refracts more than the outer layers.

The manner in which the inversion of the image is produced by a convex lens, is shown in the accompanying figure, in which the lines correspond to the rays passing from two points through the lens. If the arrow *a a′* be taken for the object, from either extremity of it rays pass through, and are more or less bent by the lens. It will be sufficient to follow the course of three rays from the head of the arrow. One of these passes through the centre of the lens, and leaves it in the same direction which it entered, because the two surfaces at the points where it entered and left may be regarded as parallel, and so cause no refraction. The rays which do not pass through the centre are bent on entering and on leaving the lens, so that they all meet at the same point and there produce an image of the head of the arrow, at *b′*. In exactly the same way the feather end of the arrow is produced at *b*; the position of the image of the object is thus reversed by the light rays passing through the lens.

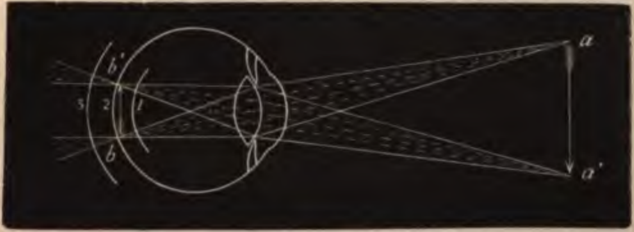


Fig. 223.—Showing the course of the rays of light from two luminous points to the retina. The rays from the point *a* on passing through the cornea, lens, &c., are collected on the retina at *b*. Those from *a′* meet at *b′*, and thus the lower point becomes the upper.

In a biconvex lens, with the two surfaces of the same degree of convexity, the central point through which the rays pass without being refracted is easily made out, as it is the geometrical centre of the lens. This central point is spoken of as the optical centre. With systems of lenses of varying convexity, and more than one in number, as we have in the eye, where the rays of light are bent at different surfaces, it is much more difficult to determine the optical centre. However, by means of the measurements made by Listing, two points close together are known, which may be said to correspond practically with the optical centres of the eye; they lie in the lens, between its centre and posterior surface. The path of the various rays may thus be exactly made out.*

The rays which come from a distant luminous point and fall upon the eye, are refracted by the cornea and aqueous humour, so as to be made *convergent* on their way to the lens; they are then further bent at the surfaces of the lens, so that they are brought exactly to a point on the retina. That is to say, for distant luminous points the retina lies exactly in the plane of focus of the dioptric media of the normal eye.

This convergence of the rays to a point on the retina, is the first essential in order to be able to see clear and distinct images; for if the rays from each point of a luminous body were not united on the retina as points, the effects of the different rays from the various points of a body would become mixed, and there would be loss of definition of its image.

The rays from any bright point which enter the eye through the pupil may be imagined to form a luminous cone, the point of which lies at the retina, and its base at the pupil. After their union at the point of the cone, the rays would diverge again if the retina were not there to receive them.

It may be seen from the foregoing figure that if the retina, which normally would lie at 2, were placed nearer the dioptric apparatus, say at 1, or further from it, at 3, it would not meet the exact point of the luminous cone, but would receive the rays either before they came to a point, or after they had diverged from it. Thus indistinct rings of light would be seen instead of one luminous point, and an image would be blurred and indefinite.

From this it follows that the eye, when quite passive, can only get an exact image of bodies which are placed at a certain distance from it, just as, for any given state of a camera, only those bodies in one plane come into focus and give a clear picture on the screen. If the dioptric apparatus of the eye were rigid and unalterable, since the relation of the retina to it is permanently the same, we could only see those objects clearly which are at a given distance from the eye. We know, however, that we get as distinct an image of distant as well as of near objects, and we can look through the window at a distant tree, or we can adjust our eyes so as to be able to see a fly walking on the window pane. However, we cannot see both distinctly at the same moment. This may be demonstrated by what is known as Scheiner's experiment, which is carried out in the following way. Two pinholes are made in a card at a distance from each other not wider than the diameter of the pupil. The card is then brought close to the eye, so that a small object—such as the head of a bright pin—can be seen through the holes. The dioptric media being fixed, moving the object nearer to or further from the eye would have the same effect as changing the relation of the retina to *m n* or *p q* in fig. 224, by means of which we may explain the following observations: (1) The eye being fixed upon the object (of which only one image is seen), move the pin rapidly away; two objects now appear, showing that the rays coming through the holes have met before they reach the retina as at *p q*. (2) Move the pin near the eye; again two very blurred objects are seen, for the rays have not met when they strike the retina, as at *m n*. (3) Keeping the object in the same position, alter the gaze, as if to look first at distant and then at near objects; in both extremes two images are seen. (4) When the object is in exact focus as at *c*, the closure of one of the holes does not affect the single image. (5) When two images are seen, closing the right hand hole at *g* causes the right or left image to disappear according as the focus *c* falls short of *m n* or is beyond *p q*, the retina. (6) By moving the pin's-head nearer the eye, a point is reached at which the object cannot be brought to a focus as a single image. This limit of near accommodation marks the near point. A little attention teaches us that looking at the near object requires an effort which looking at the distant one does not; in fact, we have to do something to see things near us distinctly. This act is the voluntary adjustment of the eye which we call its accommodation for *near vision.*

---

* The impossibility of making clear the important relationships, nodal points, and other constants of the eye in a short text book, and the deterrent effect exerted upon the mind of a junior student by brief incomprehensible statements, has induced the author to omit this part of the subject, and he must therefore refer those who are anxious to learn the cardinal points of the eye, to the more advanced text books.

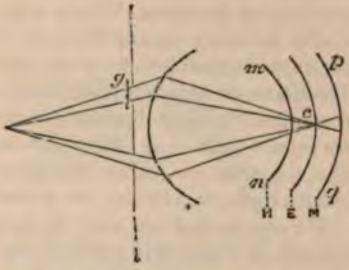


Fig. 224.—To illustrate Scheiner's experiment; for explanation, see text.

ACCOMMODATION.

The difference of distance for which we can adjust our eyes is great, so that our *range of distinct vision* is very extensive. As already stated, the normal eye is considered to be constructed so that parallel rays of light, *i.e.*, those coming from practically infinite distance, are brought to a focus on the retina. This is why we see the stars—which are practically infinitely remote from us—as mere luminous points. It is therefore impossible to fix a "far limit" to our power of distant vision. The nearer an object is brought to our eyes, however, the more effort is required to see it distinctly, until at last a point is reached where we cannot get a clear outline, no matter how we "strain our eyes." For a normal eye, called the *emmetropic eye*, this "near limit" is about 12 cm., or 5 inches, but it varies in different individuals.

For objects that are over 10 metres distance very little change in the eye is required in order to see them distinctly, and the nearer the object approaches the more frequently the adjustment of the eye has to be altered in order to see it clearly. But at every part of the range of distinct vision objects at different distances can be seen without moving the adjustment. The range of this power is measured on the line of vision, and called the focal depth. In the distance we can take in a greater depth of landscape, and this without effort or fatigue; but when looking at near objects we must constantly accommodate our eyes afresh in accordance with the shallowness of our focal depth.

The mechanisms by means of which the accommodation of the eye is accomplished, differ from anything that can be applied to an artificial optical instrument, and are much more perfect.

The changes which have been observed to take place are (1) The iris contracts so that the pupil becomes smaller; (2) the centre of the anterior surface of the crystalline lens moves slightly forwards, pushing before it the pupillary margin of the iris, and becomes more convex; (3) the posterior surface of the lens also becomes more convex but without changing its position.

These changes can be seen in the accompanying diagram, showing a section of the lens, cornea, and ciliary region (fig. 225), in the left-hand side of which the lens is drawn in the position it assumes when accommodated for near objects. These movements can be seen to take place in life by observing the changes in relative positions, &c., of the reflections of a candle flame thrown from the cornea and the two surfaces of the lens. On the cornea is seen a bright upright flame; next comes a large diffused reflection from the anterior surface of the lens, and at the other side of this a small inverted image of the flame reflected from the posterior surface of the lens. When the adjustment is changed by looking from a far to a near object, the image on the front of the lens becomes smaller and moves towards the centre of the pupil. The image on the back of the lens also becomes smaller but does not change its position. The exact amount of movement has been accurately measured by a special instrument called an ophthalmometer, and the motions can be made more obvious by means of the phakoscope, in which a dark box and prisms are placed before the observed eye, and each image is made double, so that the change in position of its two parts may be more obvious than a mere change of size.

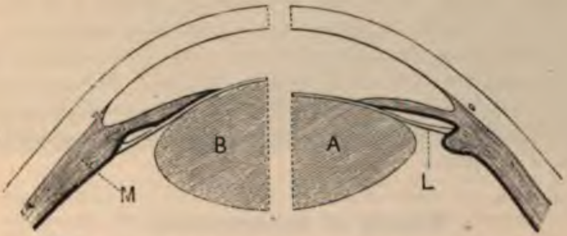


Fig. 225.—Diagram showing the changes in the lens during accommodation. The muscle on the right is supposed to be passive as in looking at distant objects, the ligament (L) is therefore tight, and compresses the anterior surface of the lens (A) so as to flatten it. On the left the ciliary muscle (M) is contracting so as to relax the ligament, which allows the lens to become more convex. This contraction occurs when looking at near objects.

The alteration in the shape of the lens is accomplished by the action of the muscular ring already named, which radiates from the edge of the cornea to the ciliary region of the choroid coat, where it is attached. The junction of the cornea and sclerotic being its fixed point, when the ciliary muscle contracts it draws the choroid coat and the connections of the suspensory ligament of the lens slightly forwards. Under ordinary circumstances, the eye being at rest, the suspensory ligament is tense and exerts a radial traction on the anterior part of the capsule of the lens, and thus tends to stretch it flat; this affects the shape of the soft lens and reduces its convexity. When the ciliary muscle shortens it draws forwards the attachment of the suspensory ligament, relaxes it, and removes the tension of the capsule, so that the unconstrained elastic lens bulges into its natural form. The posterior surface cannot extend backwards, because there it is in contact with the vitreous humour, which, if anything, is held more firmly against it by the increased tension of the hyaloid membrane during the contraction of the ciliary muscle.

The act of accommodation is a voluntary one, the nerve bearing the impulse to the ciliary and iris muscles, coming from the 3d nerve by the ciliary branches of the lenticular ganglion. The local application of the alkaloid of the belladonna plant (atropin) causes paralysis of the ciliary muscle and wide dilatation of the pupil; and the alkaloid of the calabar bean (physostigmatin) produces contraction of the muscle of accommodation and extreme contraction of the pupil.

Defects of Accommodation.

Myopia. It has been said that the "near limit" of distinct vision differs in many persons from the twelve centimeters of the normal emmetropic eye, and it is further found that the power of accommodation varies very much in different individuals. Thus "short sighted" people, who have *myopic* eyes, *i.e.*, in which distant parallel rays fall short of the retina, the near limit may only be half the normal, *i.e.*, five centimeters, and the far limit, which is normally indefinite, is found to be within a comparatively short distance of the eye. They, therefore, cannot see distant objects clearly, since the rays are focussed before the retina is reached, and then diverging cause diffusion circles and a blurred picture. The work of their accommodation is also much more laborious, since they can only see in that part of the range of accommodation where the adjustment has to be altered for slight variations of distance. The defect can be made much less distressing by the use of concave glasses, which make parallel rays strike the cornea as divergent ones, and thus allow them to be focussed on the retina.

Hypermetropia. Another abnormality is "long sight." In the hypermetropic eye, parallel rays of light are brought to a focus at a point beyond the retina, so that divergent or parallel rays cause diffusion circles and a blurred image. This may be corrected by means of convex glasses which make the rays convergent before they strike the corneal surface, and thus enable them to be sooner brought to a focus by the dioptric media of the eye.

Presbyopia is the name given to a change in the perfectness of accommodation frequently accompanying old age. The lens probably gets less elastic and the ciliary muscle weaker, so that the change in form required to see near objects is more difficult or impossible to attain. Biconvex lenses help to overcome the difficulty.

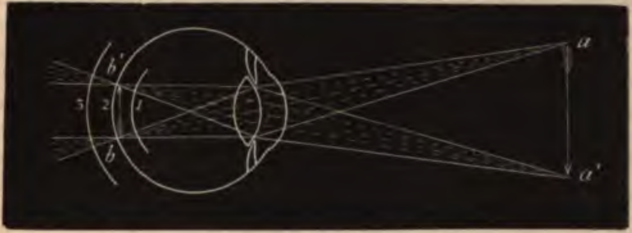


Fig. 226.—Showing the course of the rays of light from two luminous points to the retina. The rays from the point *a* on passing through the cornea, lens, &c., are collected on the retina at *b*. Those from *a'* meet at *b'*, and thus the lower point becomes the upper.

DEFECTS OF DIOPTRIC APPARATUS.

In common with all dioptrical instruments the eye has certain optical defects which tend to interfere with the exact definition of the image.

Chromatic aberration is due to the breaking up of white light into coloured rays owing to the different coloured lights, of which ordinary light is composed, possessing different degrees of refrangibility. We know this in the spectrum and in the coloured rings always seen in the marginal part of a biconvex lens made of one kind of glass, which acts like a prism. It can be corrected by making lenses of two kinds of glass, one of which counteracts the dispersion caused by the other. Optical instruments may thus be made achromatic. This defect is minimised by the iris, which cuts off the marginal rays in which it is most apt to occur. Possibly the different density of the dioptric media may have a correcting effect on the chromatism of the eye. Further correction takes place in the nerve centres which receive the sensation, for just as we mentally re-invert the image, we fail to see the colour. At any rate the chromatic aberration is so slight that it needs certain artifices to make it observable.

Spherical aberration depends upon the fact that luminous rays, on passing through a convex lens, strike the various parts of its surface at different angles, and hence are differently refracted. The rays striking the margin of the lens are more bent than those passing through the centre, and hence the former come sooner to a focus. Thus a luminous point gives rise to a diffused figure, which is circular in perfectly centered dioptric systems, or stellate in our eyes where the centering of the lenses is not absolutely accurate. Spherical aberration causes us no inconvenience, as the iris only allows the central rays to pass, upon which it can produce no noticeable influence.

Another optical defect in our eyes is *astigmatism*, depending upon some irregularity of the curvature of the cornea, which may be bent more horizontally than vertically, or *vice versâ*. In either of these cases the light in the vertical and horizontal planes will be differently refracted, so that lines drawn in the two directions will require different adjustments to see them distinctly. This may be at once recognized if we gaze with one eye at the centre from which many sharply-defined lines radiate, when only certain ones can be seen distinctly, unless we move the eye or change its accommodation. When the excessive curvature extends evenly over the whole diameter of the cornea it gives rise to what is called *regular astigmatism*, and when the unevenness is localized to one spot of the corneal surface it is called *irregular astigmatism*.

The astigmatism which may be called physiological is not noticed by the individual, but pathological astigmatism often occurs and requires cylindrical glasses to correct it.

Entoptic images are those which depend on the presence of some opacity or difference in density in the transparent media of the eye itself. They look like variously-shaped specks moving over the field of vision. They are only remarkable when we look at an evenly coloured object or through a pin-hole in a black card. In using the microscope they often annoy the unpractised observer.

THE IRIS.

It has already been mentioned that the motions of the iris alter the size of the pupillary opening through which the rays of light must pass, and while it regulates the amount of light admitted, it always cuts off a large amount of the marginal rays acting like the diaphragm of an optical instrument. The great importance of not allowing the rays which would traverse the margin of the lens to enter the eyeball can be understood after what has been said of spherical aberration. But the iris also moves so as to contract the pupil when the eye is adjusted for near vision, independently of the intensity of the light by which the object is illuminated. This action is of great advantage in viewing near objects, because the more convex the lens becomes, the more injurious are the marginal rays. If the iris did not thus contract in near vision, the nearer we brought an object to our eye the greater would be the tendency to indistinctness caused by spherical aberration.

The iris consists of a framework of delicate connective tissue, like that of the choroid coat, containing many blood-vessels. On its posterior surface is a dense layer of pigment cells called the uvea, which gives the eye its colour. The motions of contracting and dilating the pupil are carried out by smooth muscle fibres. The act of contracting the pupil is performed by a very definite set of fibres forming the sphincter which surrounds the margin of the pupil, while other fibres are said to radiate from the pupil to the attached margin of the iris. The sphincter muscle seems always to be more or less in action, because if it be paralysed the action of the dilating forces becomes obvious. But the muscular character of the dilator has been doubted from the fact that the fibres have not been satisfactorily demonstrated. Certainly the sphincter seems to be the stronger of the two, for strong electric stimulation causes contraction of the pupil, and shortly after death the pupils dilate. We must assume that the power of the sphincter dies more quickly than that of the dilator, or relaxes because it has lost the stimulus reflected from the fragile retina.

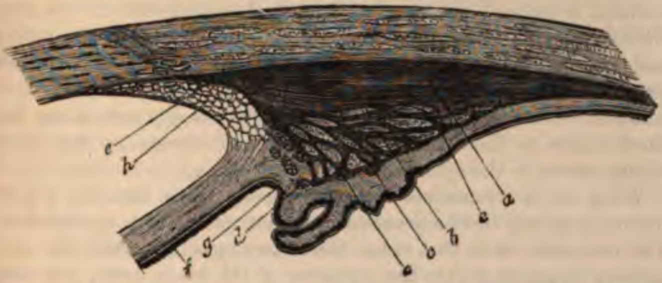


Fig. 227.—Section through the ciliary region, showing the relation of the iris (*f*) to the choroid and the ciliary muscle (*a*), which arises from the margin of the cornea at (*e*), and passes towards the choroid to the right where it separates the latter from the sclerotic.

The nerves supplying the dilator muscle seem to be derived from the sympathetic, for when the sympathetic in the neck is cut, the pupil remains permanently contracted. These fibres are supposed to take origin in the grey matter of the cervical spinal cord. The sympathetic also supplies the muscles in the walls of the vessels, and thus controls the amount of blood going to the iris. Though the variation in blood supply may co-operate in causing dilatation, it cannot be the only cause, as the widening of the pupil may be caused in a bloodless eye.

The nerve mechanism by which the sphincter muscle is made to contract is quite distinct, and more definitely understood. Its contraction is a reflex act, the stimulus of which starts in the retina and travels along the optic nerve as an afferent channel to the corpora quadrigemina, where there is one centre governing the contractions of both irides. The efferent impulses are sent along the third nerve to the lenticular ganglion, and thence by the short ciliary nerves to the eyeball.

When we accommodate for near objects three muscles act in unison, so we say their movements are "associated" with one another. The voluntary effort that causes the ciliary muscle to relax the suspensory ligament, makes the sphincter of the iris contract, and also stimulates the internal rectus to move the eye inwards. The voluntary nerve centre must be in intimate relation to the reflex centre, which keeps up the tonic action of the sphincter iridis.

We have then central nerve governors for the ciliary and iris movements. The ciliary muscle and sphincter of the pupil are together stimulated by the will, and the sphincter alone is excited by means of a centre which reflects the stimulus arriving from the retina by the optic nerve along the branches of the third nerve. The dilator of the pupil, if a muscle, is also kept in gentle tonic action by the impulses sent from the spinal marrow, *viâ* the sympathetic, with the vaso-motor impulses; but some think that the blood supply and tissue elasticity explain the dilatation.

From the facts (1) that reflex contraction of the pupil may be produced by stimulating the retina, even when the eye is cut off from the brain centres, and (2) that the local effect of atropia in dilating and calabar bean in narrowing the pupil, seem in a measure independent of the central nerve organs, it has been concluded that there must be some local nerve mechanism in the eye itself capable of reflecting nerve stimuli and being affected by these poisons.

The student must never lose sight of the circumstances under which the pupils contract, namely :—

1. The application of strong light even to one retina, causes reflex stimulation of the ciliary nerves.

2. Stimulation of the nasal and ophthalmic branches of the fifth afferent nerve excites the sphincter.

3. Contraction of the pupil is "associated" with accommodation for near objects.

4. Similar "associated" contraction, accompanies inward movement of the eyeball.

5. During sleep, or as the result of vasomotor disturbances in the brain (anæmia), the pupil contracts.

6. Under the influence of physostigmatin, nicotin, and morphia.

7. From any stimulation of the optic or third nerves or the corpora quadrigemina.

The circumstances in which the pupils are found to be dilated are equally important from a practical point of view, namely :—

1. In the dark or with insensitive retinæ.
2. Irritation of the cervical sympathetic.
3. Under the influence of atropin, daturin, &c.
4. In asphyxia or dyspnœa from venosity of the blood.
5. Painful sensations from the skin, &c.

THE OPHTHALMOSCOPE.

When we look into the eye the pupil appears quite black, because the illumination of the eye-chamber is not sufficient to show its parts from the outside, when the light is strong. In the same way *when we try to look* into a room in the daytime through the

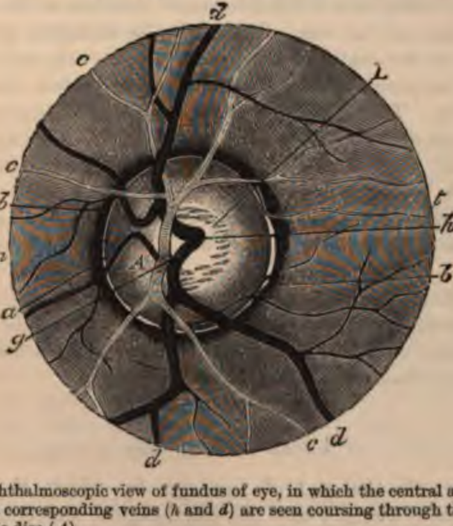


Fig. 228.—Ophthalmoscopic view of fundus of eye, in which the central artery (*g* and *c*) and the corresponding veins (*h* and *d*) are seen coursing through the retina from the optic disc (*A*).

window we see nothing in the depth of the room, because the lig outside is so much stronger than that within the room. If, howeve we look in at night, when the room is lighted up while it is dark ou side, we can see every object clearly. So if we illuminate the insi of the eye by any means we shall be able to see the details of th inside of the eye-chamber.

This means is supplied by the ophthalmoscope, which reflects th light from a lamp into the chamber of the eye so as to illuminate i completely, and when the surroundings are not too bright, the fundu of the eye can be clearly seen and investigated. A lens is usuall interposed between the eyes of the observer and the observed, i order not only to illuminate but also to magnify the fundus an enable the observer to see all the details of the parts. With thi instrument a round whitish part is seen a little to the nasal side o the axis of the eye, where the nerve pierces the dark choroid coa This is called the optic disc. The fundus now, when lighted up, does not look black, but is of a lurid red colour, owing to the grea vascularity of the choroid coat. Over this red field are seen a number of blood-vessels, which start from the centre of the opti disc, and radiating over the fundus send branches to the most anterior parts that can be seen. These are the branches of the vessel which runs in the centre of the nerve. In the very axis of the eye a peculiar depression, free from branches of the blood-vessels, can be seen. This central depression (fovea centralis) differs a little in colour from the neighbouring parts during life, an turns yellow at death, and hence has been called the "yellow spot." The retina is so transparent that we cannot see it with the ophthalmoscope, but the radiating vessels (central arteries and veins of the retina) lie in it and belong to the nervous structure only.

The ophthalmoscope has proved of inestimable value not only to the ophthalmologist but also to the physician, as a means of arriving at an accurate knowledge of disease. Hence it has become mo a pathological than a physiological instrument.

LIGHT IMPRESSIONS.

The retina is the part of the eye by which the physical motion—light is changed into the physiological phenomena known as nerve impulse, by means of which the impression of light i excited in the brain. In reaching the retina the light is not i any way altered from the light with which physicists experiment but at the retina this physical motion is stopped. The optic nerves no more convey the light waves from the eye to the brain than the tactile nerves carry the objects that stimulate their endings, but only send a nerve impulse which the retina, on its exposure to the light, excites in the optic nerve. As already stated, any form of stimulation will cause the same kind of impulse to pass to the brain and there set up the same sensation of light. Thus we are told by persons who have had their optic nerves cut that the section was accompanied by the sensation of a flash of light. Any violent injury of the eye-ball causes a flash of light to be experienced. This fact has long since been arrived at in a practical manner, for a blow implicating the eye-ball is vulgarly said to "make one see stars." Also, without violent injury, if we close the eyes and turn them to the left side and then press with the point of a pencil on the right side of the eyeball through the lid, we have a sensation of a point or ring of light on the opposite side of the eyeball. Thus we say that the specific energy of the optic nerves excites a sensation of light, and the adequate stimulus of the organ of vision is light. The first question that arises is, what part of the retina does this important work of stimulating the optic nerve when light impinges on its terminals?

THE FUNCTION OF THE RETINA.

The retina is not a simple sheet of nerve fibrils or of nerve cells, but a most complex peripheral apparatus, which to histologists has offered an endless field of study. This complex body is spread all over the fundus of the eye except at the optic disc, where the nerve pierces all the coats of the eye; here there is nothing else but nerve fibres and hence no retina properly so called.

The structure of the retina varies in different parts, but it may be said to be composed in the main of the following layers. The exceptions will be mentioned afterwards, viz.:—(Compare fig. 216.)

Lying next to the hyaloid membrane is the layer of *nerve fibres* which radiate from the optic disc to the ora serrata near the ciliary region. The fibres spread evenly over the fundus except at the central point (fovea centralis), which they avoid by passing on each side of it.

Next to the fibres comes a layer of *nerve cells*, these seem commonly to have one pole connected with a fibre from the optic nerve, while from the other side two or three poles send processes into the other layers of the retina.

Then comes an indistinct layer made up of granular material a two layers of peculiar nuclear bodies, with a layer of granul material between them.

Outside of these, and separated by a fine limiting membrane, is t most important layer of the retina. It consists of a layer of r *and cones* which are connected with those parts of the retina alrea named, and seems project into the p toplasm of pigment cells of epitheli character, which, their outer face, sh a striking hexagon outline.

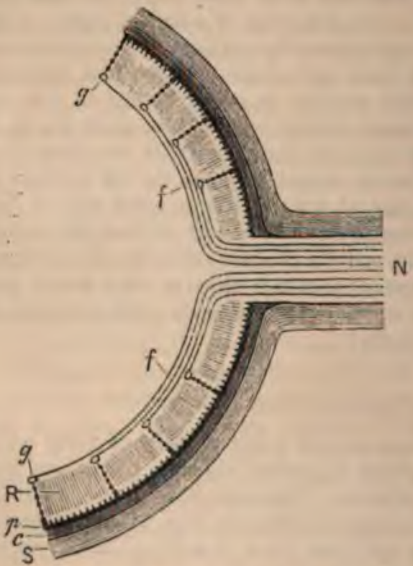


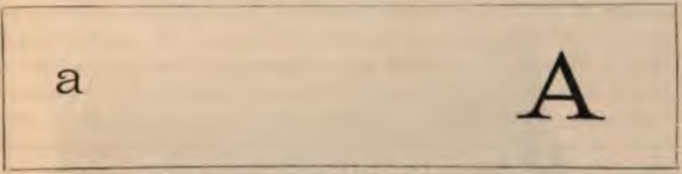
Fig. 229.—Showing the course of the fibres of the optic nerve N, as they pass along the inner surface of retina R, to meet the ganglion cells g, whence special communications pass outwards to the layer of rods and cones in the pigment layer p, next the choroid c.

A nerve fibril th may be said to ha the following cours entering with the oth fibrils at the po *opticus*, it reaches t immediate vicinity the hyaloid membran and runs a certa distance in conta with that membra it then turns outwar towards the chor and enters a ne cell. From the ne cell pass on a couple filaments which pie the various granular a nuclear layers—wh they probably fre inosculate with t fibrils from other cells—and finally terminate in a rod or a co The rods and cones may then be regarded as the ultimate termin of the nerves, and they lie in the active protoplasm of the peculi pigmented epithelium cells.

It is this outer layer, consisting of rods and cones lodged in epith lial protoplasm, which is the really effective part of the retina. Of th we have the following evidence :—

1. The fact that the rods and cones must be regarded as the real anatomical nerve terminals of the optic nerve.

2. Where the optic nerve enters the eyeball and the nerve fibres are fully exposed to the light, there are no rods and cones. This part, the optic disc, cannot appreciate light, and hence is called the "blind spot." This fact shows that the nerve fibres are quite insensitive to light, and that we must look to the terminals for its appreciation. The existence of the blind spot can be demonstrated as follows. Shut the left eye, and hold the left thumb, at ordinary reading distance, in front of the right eye. While the eye is fixed on the left thumb bring the right thumb within about four inches of it and move it slowly an inch or so from side to side. A little practice soon finds a place when the right thumb nail disappears. It also can be demonstrated by steadily fixing the right eye on the small letter "**a**" and moving the page to or from the eye very slowly; a distance may thus be reached when the large letter "**A**" is quite lost. On approaching the page—the eye still fixed on "**a**"—"**A**" reappears from the inner side; on withdrawing the page it comes into view from the outer side. This blind spot is not noticed in ordinary vision as we have habitually overcome the deficiency since infancy by our judgments being derived from two eyes. By rapid movements one eye hides the deficiency, as seen when attempting the experiment just described.



3. The fact that when the eye is illuminated in a peculiar way we can see the shadow of the blood-vessels which lie in the inner layers thrown upon the outer layer of the retina, also shows the latter to be the sensitive one. This phenomenon, known as PURKINJE'S FIGURES, can be demonstrated as follows. Close the left eye in a dark room, with an evenly dull-coloured wall, and while you stare fixedly at the wall hold a candle so that the light can reach the fundus of the eye from the side. With a little practice the least motion of the candle will bring out an arborescent figure on the wall, which exactly corresponds to the retinal vessels. It may also be seen by arranging a microscope so as to show a bright light—on

looking into the instrument and either moving it or the head slightly but constantly—the shadows of the retinal vessels will be clearly seen as though they were under the instrument.

4. The yellow spot, where the retina is chiefly made up of the cone layer, is very much the most sensitive part of the retina, and, nearest the ora serrata, where the rods and cones are but badly developed, sight is least acute.

As in the perception of two points of contact, so we find the retina ceases to be able to distinguish the difference between two luminous points, if they be brought to a focus at a distance of less than ·002 mm. from one another. This distance nearly corresponds to the diameter of the cones, and it is supposed that the rays from two luminous points must come upon two different cones in order to be visible as two distinct objects. The cones are, however, very irregularly distributed over the retina, being packed closely together at the yellow spot, and scattered more and more widely apart as one passes to the peripheral parts of the retina. It is only at the yellow spot in fact that the cones, which here are very thin, are so close together as ·002 mm., so that this estimation of the size of visual areas only could hold good of the yellow spot, and towards the peripheral parts the power of discrimination must be much less keen. This is found to be the case, for in ordinary vision everything seen clearly with a sharp outline must be brought upon the yellow spot.

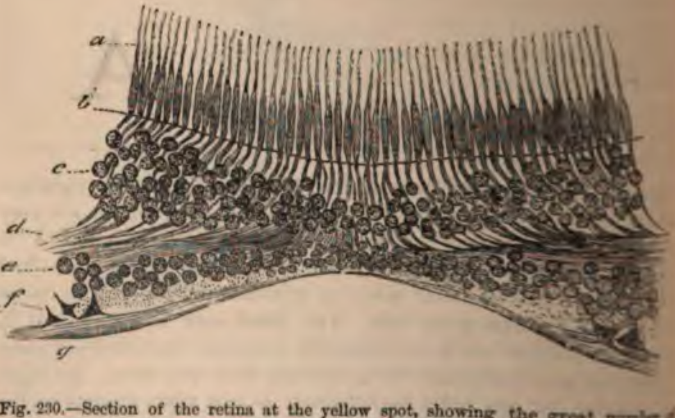


Fig. 230.—Section of the retina at the yellow spot, showing the great number of cones (*a*) at this point, and the thinness of the other layer. (Cadiat.)

This is spoken of as "direct vision." The images falling on the other parts of the retina are but dim and indistinct outlines, and these are spoken of as "indirect vision."

The stimulus need only be applied for a very short time in order to cause a distinct sensation, for we can distinctly see a single electric spark; it need only be applied to an extremely small part of the retina, as we can, by direct vision, see a very minute speck of light, and a very feeble ray suffices to stimulate the retina. The amount of stimulation produced depends upon (1) the intensity of the light, *i.e.*, the amount of light received in a given area; (2) the duration of its application; and (3) the extent of retina to which it is applied; (4) the part of the retina stimulated; (5) the darker the background the weaker the illumination we can distinguish, *i.e.*, the greater the stimulating effect of a weak light; (6) by fatigue the retina loses its power of appreciating light, and more stimulus is required to produce a given effect. On waking, the daylight is at first dazzling, but soon the retina can bear the stimulus. An increase of intensity of light does not cause an exactly proportional increase of stimulation, for we find the more the light is intensified the less are we able to notice a fresh increment of light until a degree of intensity is arrived at, when no further addition can be detected, and the light becomes blinding. The less the absolute intensity of two lights the better can we distinguish any difference that may exist between them.

The effect lasts for a noticeable time after the stimulus has been removed, particularly if the light be very intense. This can well be seen when a brilliant point is observed in rapid motion; instead of a point a streak of light is seen. Thus falling stars leave a line of light after them caused by the persistence of the stimulus, and a luminous body rapidly rotated gives the impression of a circle of fire and not of a moving point.

When the stimulus is very intense, such as is caused by an electric light or when we look at a bright object like the globe of a lamp steadily for some time, then the effect persists for a very considerable time, and even after the eyes are shut we see a distinct image of the object. This is called the *positive after image.* If the retina be exposed to a bright light until it be fatigued, and then suddenly turning we gaze at a white wall, the bright part of the positive after image is replaced by a dark figure which is termed the *negative after image.*

A strong stimulus applied to the retina spreads from the part upon which the bright image falls to the parts in its immediate neighbourhood, so that the bright object looks larger. This phenomenon is called *irradiation*. It helps to explain many of the peculiarities of vision.

The question now arises, how does the retina, or rather its layer of rods and cones, convert light into a nerve stimulus? It would appear quite out of the question that the 456 to 700 billions of waves of light per second could mechanically excite the nerve terminals as the waves of sound excite the endings of the auditory nerve. But we know that light has a very distinct action on many chemical combinations, such as reducing salts of silver and gold, &c. We, therefore, imagine that the light waves set up, in the outer layer of the retina, certain intermolecular motions or chemical interchanges, the result of which is that the nerve fibres are stimulated to activity and transmit an impulse to the brain. In the outer layer of the retina the light may be said to produce a change in the retina which in some respects may be compared to that which occurs on the sensitive photographic plate, when exposed, in a camera. In some respects only, however, because there is this great difference that while the chemical change on the sensitive plate persists so as to give rise to a photograph, in the eye, on the other hand, it only lasts during the brief moment during which we can recognize the positive after image. The chemical explosion in muscle may be compared to the explosion of gunpowder, in giving rise to force, but not in the result to the materials. For in muscle as the chemical change which causes the contraction is rapidly repaired, so in the retina a new sensitive plate is at once produced by the restoration of the normal condition of the molecules.

The idea that the layer of rods and cones undergoes some chemical change on exposure to light which suffices to induce excitation of the optic nerve, has received great support from the observation that a colour of a red or purplish hue exists in the outer part of the rods and that this changes when exposed to the light. But this so-called *visual purple* cannot have a very inseparable connection with vision, since it is absent where the retina is most sensitive, *i.e.*, the fovea centralis, where there are no rods, and further, frogs with blanched eyes seem to see quite well.

The peculiar pigmented epithelial cells of the retina have been observed to change their shape slightly, and definitely to alter the position of the pigment granules they contain when exposed to light. When we remember how sensitive to light the protoplasm of many unicellular infusoria is, we cannot be surprised that the protoplasm of the retinal epithelium is affected by it. Moreover in the pigment cells of the frog's skin we are familiar with a change in shape and in the arrangement of their pigment granules in response to different light stimuli. We know that in the nervous centres nerve impulses are commonly originated by protoplasm under the influences of slight changes in temperature or nutrition. It would be hardly too much to assume, then, that the retinal epithelium has some important share in the transformation of light into a nerve stimulus. The arguments pointing to the rods and cones as the essential part of the retina apply equally well to the pigmented epithelium, for they are so dovetailed one into the other that they form but one layer. They are not known to be connected with the nerve fibres, but even supposing they be not in any way connected with the nerves they might still be influenced by the light, and by some kind of motion communicate the effect to the contiguous sensitive nerve terminals, which are elaborately adapted to appreciate subtle differentiations of stimulus.

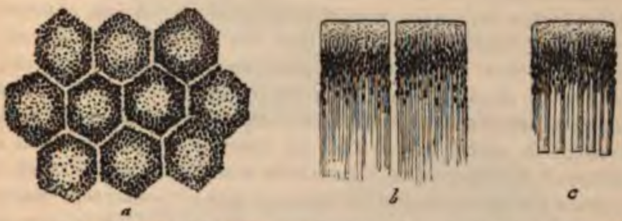


Fig. 231.—Epithelial cells of the retina. *a*, Seen from the outer surface; *b*, Seen from the side as in a section of the retina; *c*, shows some rods projecting into the pigmented protoplasm.

COLOUR PERCEPTIONS.

If a beam of pure white sun-light be allowed to pass through an angular piece of glass or prism it is decomposed into a number of colours which may be seen by looking through the prism, or may be thrown on a screen, like that of a camera. These colours, which look like a thin slice of a rain-bow, are together called the *spectrum.* The white solar light is thus shown to be a compound of rays of several colours which possess different degrees of refrangibility and hence are separated on their way through the prism. The violet rays are the most bent, and the red the least, so that these form the two extremes of the visible spectrum. The difference of colour depends upon the different lengths of the waves, the vibrations of violet (667 billions per sec.) being much more rapid than those of red (456 billions per sec.) Beyond the visible spectrum at the red end there are ot rays which though they look black to the eye, are capable of trans ting heat. This thermic power is best developed in these ultra-red ra and fades gradually towards the middle of the spectrum. Outside th violet are ultra-violet rays, which, though non-exciting to the retin are very active in inducing many chemical changes. Only those of vibrations which have a medium length, can stimulate the retina.

If two different colours be mixed before reaching the retina, or applied to it in very rapid succession one after the other an impressi is produced which differs from both the colours when looked separately; thus violet and red give the impression of purple, colour not in the spectrum. If all the colours of the spectrum in th same proportion and with the same brightness fall upon the retin the result is white light. This we know from the common e perience of ordinary white light which is really a mixture of all th colours of the spectrum, and we can see it with a "colour top" paint to imitate the colours of the spectrum. When the top is spinnin the colours meet the eye in such rapid succession that the stim of each falls on the retina before that of the others has faded aw and thus many colours are practically applied to the retina at th same time, and the top looks nearly white.

It has been found that certain pairs of colours taken from th spectrum when mixed in a certain proportion produce white. The are *complementary* to one another. The complementary colours are :-

Red and peacock-blue
Orange and deep-blue
Yellow and indigo
Greenish-yellow and violet.

If colours which lie nearer to each other in the spectrum than th complementary colours be mixed, the result is some colour which i to be found in the spectrum between the two mixed.

The perception of the vast variety of shades of colour that we ca distinguish, can only be explained by means of this colour-mixin We assume that there are three primary colours which overlap o another in the spectrum so as to produce all the various tints. The are *red*, *green*, and *violet*; the arrangement of which may be th diagrammatically explained (fig. 232).

We must further assume that there are in the retina three speci sets of nerve terminals, each of which can only be stimulated by re green, or violet respectively, and the innumerable shades of colou we see, depend upon mixtures of different strengths of these primar colours, so as to produce different degrees of stimulation of each set nerve terminals.

The view that such special nerve apparatus do exist for red, green, and violet is supported by the fact that the most anterior or marginal part of the retina is incapable of being stimulated by red objects which, therefore, look black when only seen by this part of the retina. This inability to see red may extend over the whole retina as is found in some persons who may be said to be, red-blind. Moreover if we investigate our negative after images, after looking for a long time at a red object, we find them to be greenish blue. That is to say, the nervous mechanism for receiving red impressions is fatigued, and consequently those of its complementary colour are easily stimulated.

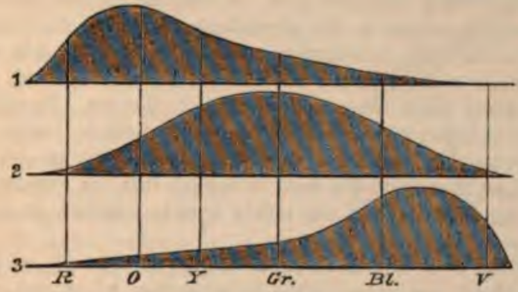


Fig. 232.—Diagram of the three Primary Sensations: 1 = red; 2 = green; 3 = violet. The letters below are the initials of the colours of the spectrum. The height of the shaded part gives extent to which the several primary sensations are excited by different kinds of light in the spectrum.

Mental Operations in Vision.

Our visual sensations enable us to perceive the existence, the position, and the form of the various objects around us. For the perfection of a visual perception much more is necessary than the mere perfection of the dioptric media of the eye, and of the retinal nerve-mechanisms. Besides the changes produced in the retina by the light, by means of which the optic nerve is stimulated, and the excitations produced, by the impulses passing along the nerve, in the nerve cells of the seeing centre, there must be further a psychical action in other cells of the cortex of the brain. This psychical action of the brain consists of a series of conclusions drawn from the experiences gained by our visual and other sensations.

Our ideas of external objects are not in exact accord with the image produced on the retina and transmitted to the brain, but are the result of a kind of argument carried on unconsciously in our minds. Thus when no light reaches the retina, we say (without what we call thought) that it is dark; our retina being unstimulated, no impulse is communicated, and the sensation of blackness arises in our sensorium. When luminous rays are reflected to the retina from various objects around us, the physiological impulse starts from the eye, but in the brain, by unconscious psychical activity it is referred in our minds to the objects around us, so that mentally we project into the outer world what really occurs in the eye. So also, from habit, we re-invert in our minds the image which is thrown on the retina by the lens, upside-down, and so unconscious are we of the psychical act that we find it hard to believe that our eyes really see every thing inverted, and our minds have to reinstate them in the upright position.

One of the most important means employed to enable us to form accurate visual perceptions is the varied motion which the eyeballs are capable of performing.

MOVEMENTS OF THE EYEBALLS.

The eyeballs may be regarded as spherical bodies, lying in loosely fitted sockets of connective tissue padded with fat, in which they can move or revolve freely in all directions, in a limited degree. The muscles which act directly on the eyeball are six in number. Four recti muscles, which pass from the back of the orbit and are attached to the eyeball, one at each side and one above and below, not far from the cornea, can move the front of the eye to the right or left, and up or down respectively; and two oblique muscles which pass nearly horizontally outwards, and a little backwards, and are attached to the upper and under surface of the eyeball respectively. These muscles can slightly rotate the eye on its antero-posterior axis, the upper one drawing the upper part of the eyeball inwards and the lower one, as its antagonist, drawing the lower part inwards, so as to rotate the eyeball in an opposite direction on the same axis.

The internal and external recti draw the centre of the cornea towards or from the median line respectively, directly opposing one another.

On account of the direction of the superior and inferior recti being different from that of the axis of the eyeball, they draw the outer edge of the cornea, not its centre, up and down respectively, and at the same time tend to give the eyeball a slight rotation in the same direction as the corresponding oblique muscles. The tendency to rotation is counteracted by the antagonistic oblique muscle when simple elevation or depression is performed.

Thus pure abduction or adduction only requires the unaided action of the internal or external recti, while direct depression of the eye requires the combined action of the inferior rectus and superior oblique, and direct elevation requires the superior rectus and inferior oblique to act together. The various oblique movements are accomplished by various combined co-ordinations of movements of the different muscles.

The diagram shows the directions towards which the different muscles tend to draw the centre of the cornea from the straight position.

From this it is obvious that the commonest movements of the eye require the co-operation of different muscles.

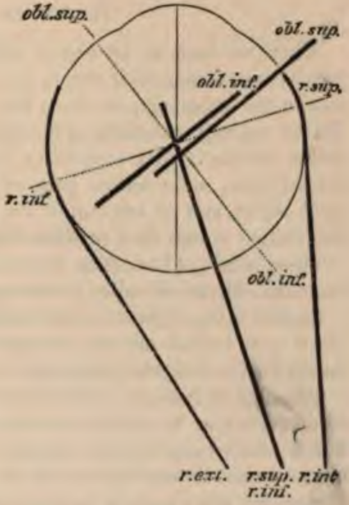


Fig. 233.—Diagram of the direction of the action of the muscles of the eyeball, which is shown by the dark lines. The axes of the rotation caused by the oblique and upper and lower recti are shown by the dotted lines. The inner and outer recti rotate the ball on its vertical axis, which is cut across. The abbreviated names of the muscles are affixed to the lines.

In the ordinary movements of the two eyes more than this is necessary. The two eyes must move in the same direction at the same time, now to the right, now to the left, so that while the external rectus moves the right eye to the right side, the internal rectus moves the other eye in the same direction. We say then that the co-ordination of the movements of the muscles of the eyeball is so arranged, that the contractions of the external and internal recti of opposite sides always occur in association, and we call these "associated movements." This association of movement has been acquired by the habit of voluntarily directing the two eyes at the same object, and has gradually become involuntary, for few persons have the power of exerting voluntary control over the muscles of or other eye alone.

BINOCULAR VISION.

When we look at an object with both eyes we have a separ image thrown upon each retina, and therefore two sets of impulses sent to the sensorium, one from the right and one from the left Yet we are only conscious of the occurrence of one stimulation. T reason of this is, that experience has taught us that similar ima thrown upon some certain parts of the two retinæ correspond to same object, and in our minds we fuse the sensations caused by two images so that they produce but one idea.

These points of the retina which are thus habitually stimulated the same objects are called "corresponding points."

Besides being of great use in making up for such deficiencies as t blind spots (which are not corresponding points) binocular vision useful for the following purposes :—

To judge of *distance.* When using one eye only, some knowled of distance may be gathered by the force employed to accommoda but a much more accurate judgment can be made when both e are used and the muscular sense of the ocular muscles, employed converging the eye-balls for near objects, can be used as evidence their distance.

In judging of *size*, in the same way, with one eye, we can only ha an idea of the apparent size of an object, which will vary with distance. With a knowledge of the apparent size and of the dista such as is gained by binocular vision, we can come to a fairly accura conclusion as to the size of an object.

To judge of the relative distances of objects so as to see *depth* the picture before our eyes, binocular vision is necessary. If one alone is used we see a flat picture without having an accurate idea the relative distances of the different things we see. With each however, we get a slightly different view of each object, and thus are helped to conclude as to their exact distances and shapes, to be able to arrive at fairly correct judgments as to their ou form, &c.

CHAPTER XXXIII.

HEARING.

JUST as impulses travelling along the optic nerves can only give rise, in the sensorium, to impressions of light, so impulses communicated to the *portio mollis* of the seventh pair of cranial nerves can only excite impressions of sound, and any stimulation of that nerve gives rise to sound sensations.

The peripheral end of the special nerve of hearing is distributed to an organ of very peculiar construction situated in the internal ear, which, from its complexity, has been called the *labyrinth*. The nerve-ending is spread out between layers of fluid, so that it must be affected by very gentle forms of stimulation ; and when we know its delicacy, we can hardly be surprised that even sound vibrations suffice to stimulate this terminal to transmit a nerve impulse to the brain. But the organs of hearing of mammalia and man are so deeply placed in the petrous part of the temporal bone, that a special mechanism has to be adopted to convey the sound with sufficient intensity from the air to the fine nerve-terminals. These beautiful contrivances make up a complex piece of anatomy which will be briefly referred to presently.

SOUND.

Before attempting to describe the complex mechanisms by means of which the sound is conveyed to the nerve-endings, some notion must be formed of what sound is from a merely physical standpoint. Without the sense of hearing one cannot form any idea of sound, and here the knowledge of sound ends with many people, since they only think of it as something they can hear. A physicist, however, regards sound in a very different way. He knows that it is caused by a kind of motion known as the vibrations of elastic bodies, such as a tense string, a metal rod, or an elastic membrane. These vibrations, being communicated to the air, are conveyed by it to our ner endings, where they set up a nerve impulse. The impulse is tra mitted along the nerve to the brain, and there gives rise to t sensation with which we are familiar as sound.

The vibrations of the air are wave-like movements depending up a series of changes of density in the gases, the particles of which mo towards or from one another, and transmit the motion to their neig bours, so as to propagate the sound wave. To demonstrate th vibrations a special apparatus must be used.

When a tuning fork is struck it is thrown into vibration, and sound is given forth. But the vibrations are often so rapid and so sma that the motion of the tuning fork cannot be appreciated by the ey But if a fine point be attached to one prong of the tuning fork— indeed, any elastic body, such as a bar of metal—and this po be brought into contact with a moving smoked surface, such as h been already described for similar records, a little wavy line drawn, showing that the vibrating fork moves up and down an even and regular rate. Each up and down stroke indicate vibration. The length of the wave, as drawn on the evenly-movi surface of the recorder, shows the amount of time occupied by ea vibration. This is always found to be the same, for a tuning fork a given pitch, and thus the recording fork is in constant use by th physiologist as an exact measure of small intervals of time. Th *pitch* of the note, then, depends upon the *rate* or *period* of vibratio a note or tone of a certain pitch being simply a sound caused by many vibrations per second. The quicker the vibration the high the note, and the slower the deeper, until at the rate of about thir per second, no sound is any longer audible. Whether a note be pr duced by a metal fork, a tense string, or any other vibrating body, the number of vibrations per second be the same, the note must hav the same pitch.

The elevation of each vibration as seen in the tracing made by recording fork is different at different times. When the fork is fi struck, the waves are high and well marked, and the excursions the recording prong can be seen to become less and less extensive the fork gradually ceases to vibrate, and the sound becomes faint; in other words, as the sound produced becomes less loud, the vib tions are smaller, and the amount of excursion made by t vibrating body is commonly spoken of as the *amplitude* of the vib tion, and upon it alone depends the *loudness* of the sound. Th the pitch of a tone bears no relation to the amplitude of the wave the vibration, but depends upon their rate; while its loudness quite independent of the period occupied by the vibrations, but is in proportion to the extent or amplitude of the waves.

So far only *tones* or musical notes have been mentioned. They are produced by vibrations occurring at perfectly regular periods. The simpler and more regular the vibrations, the purer the tone. But the great majority of the sounds we are accustomed to hear are not pure tones, but are the result of an association of vibrations bearing more or less relation one to the other. When the variety of vibrations is very great, their intervals irregular and out of proportion, they give rise to a discordant sound devoid of musical tone, which is commonly called a noise. But so long as such commensurability exists in the rate of the vibrations as to produce a sound not disagreeable to the sense of hearing, it may be called a note.

By the use of a series of different resonators, each of which is capable of magnifying a certain tone, it can be shown that the clearest and purest notes of our musical instruments are far from being simple tones, but are really compounds of one prominent note or fundamental tone, modified by the addition of numerous *over-tones* or harmonics. If one blows forcibly across an orifice leading to a space in which a small amount of air is confined, such as the barrel of a key or the mouth of a short-necked flask or bottle, either a clear shrill or dull booming sound is heard, which varies in pitch according to the proportions of the air-containing cavity. This dull note is a simple tone. It is devoid of character, and in this respect differs greatly from the notes produced by a musical instrument. The notes of every instrument have certain characters or qualities which enable even the most unpractised ear to distinguish them from one another.

This peculiar *quality*, which is independent of the pitch (*i.e.*, rate of vibration) or the intensity (*i.e.*, amplitude of wave), is called the *colour* or *timbre* of the note. It depends on the number, the variety, and the relative intensity of the over-tones or harmonics, which accompany the notes. So that really the *timbre* or quality of a note, and therefore the special characters of the different musical instruments, is produced by their impurity, or the complexity of the overtones which aid in producing them.

All elastic bodies can vibrate, and therefore are more or less capable of conducting sounds. Sound vibrations can be transmitted from one body to another placed in contact with it. From a hard material the waves are readily communicated to the air, and this is the ordinary medium by means of which sound is transmitted and finally arrives at our organs of hearing. The old experiment of placing a small bell under the glass of an air-pump and making the tongue strike it after the air has been removed, shows that the medium of the air is essential for the transmission of the sound-vibrations.

The transmission of waves of sound from the air to more dense materials, such as those which surround our auditory nerve-terminals, takes place with much greater difficulty than that from a solid to the air, and we find a variety of contrivances by which the gentle waves, arriving at the ear by the air, are collected and intensified on their way to the labyrinth.

But the medium of the air is not necessary in order that sound may reach the internal ear. Nor is the route through the outer canal, and the drum and its membrane, the only one by which the vibrations can arrive at the cochlea. The solid bone which surrounds the labyrinth is in direct communication with all the bones of the head, and the sound can travel along these bones and reach the nerve-endings. This can easily be proved by placing the handle of a vibrating tuning fork against the forehead, or better still, against the incisor teeth. The sound, although previously hardly audible, at once becomes quite distinct, or even appears loud.

This direct conduction through the bones of the head is, under normal conditions, of little use to man; but attempts have been made, in cases where the ordinary auditory passages were rendered inefficient by disease, to gather the vibrations on a vibrating plate or tympanum, and apply this to the teeth. This direct conduction of sound is, however, very valuable in determining the seat of the disease in cases of deafness. So long as a clear sensation of sound reaches the brain through the bones of the head, one knows that the important nerve-endings and their central connections are unimpaired, and can then conclude that the disease lies in the mechanical conducting parts of the hearing organ.

In fishes, where the labyrinth is the only part of the auditory apparatus which exists, it is embedded in the cranium, and the sound waves arrive through the medium of water, and are directly conveyed to the nerve-endings by the bones of the head. An air-containing tympanum would be a great impediment to the hearing of these animals.

CONDUCTION OF SOUND-VIBRATIONS THROUGH THE OUTER EAR.

The parts of the ear through which the sound commonly passes before it reaches the nerve, are naturally separated into three, viz.: (1) the external ear and the auditory canal; (2) the middle ear.

tympanum or drum, which is shut off from the latter by the tympanic membrane ; and (3) the fluid of the labyrinth.

In man, the ear muscles are so poorly developed that he can hardly move the external ear or pinna perceptibly, and the part commonly called the ear is of little use. We know this, because the outer ear may be quite removed without materially affecting the power of hearing. Birds hear well without any outer ear, and the sound reflected from the pinna may be excluded by placing a little tube in the auditory canal without reducing the intensity of the sound. But the moveable ears of many animals are, no doubt, useful in helping them to ascertain the direction from which a sound arrives, by catching more of the vibrations coming to their orifice. That the external ear may be of some use, even to man, one is led to believe, by the natural readiness with which a person with dull hearing supplements it by means of his hand. But in this act the ear is commonly pushed away from the head to an angle of about forty-five degrees, and thus its projection is considerably increased.

The auditory canal is a crooked and irregular passage, getting rather wider as it approaches the tympanic cavity. It is usually the seat of some short, stiff hairs, which help to prevent the entrance of foreign matters. It is supplied with a peculiar modification of sweat glands, which secrete a waxy material that helps to keep the walls of the canal and the outside of the membrane moist and soft. Upon the more ordinary sound-vibrations, however, the auditory canal has little or no effect. The elastic column of air in any circumscribed space resounds more readily to some one certain tone, which varies according to the capacity of the space ; thus are formed resonators of different pitch. Just as different tubes or key barrels have different notes when blown into, so the auditory canal has a note of its own, and if the canal be short, the note is one of a very high pitch. When a tone of the same pitch as that to which the canal is tuned strikes the ear, it is unpleasantly magnified, and it is said that such sounds are those which we commonly call shrill and disagreeable.

The end of the auditory canal is closed by the *membrana tympani*, which slopes obliquely from above downwards and inwards, by which means its size is greater than if it were directly across the canal. This membrane is not flat, but the central point is drawn in by the handle of the *malleus*, which is firmly attached to it along its entire length. The membrane is thus held in the shape of a very blunt cone, somewhat like a Japanese umbrella, the apex of which points inwards towards the cavity of the drum. The peculiar form of the membrane of the drum is of great importance for distinct hearing.

As every confined volume of air has a certain tone of its own to which it resonates more readily than to others, so a membrane of a given size and tension has a certain *self-tone*, the vibration periods of which it follows with great ease. This tone varies with the tension, as may be seen in a common drum, the note of which can be changed with the tension of its parchment—the tenser the membrane, the higher the pitch. If the membrane of the drum of our ears were thus set to one tone, our hearing would be most imperfect and unpleasant, for we should be wearied by the reiteration and persistence of the note to which the tympanic membrane was tuned. But this does not occur; the tympanic membrane has no self-tone,

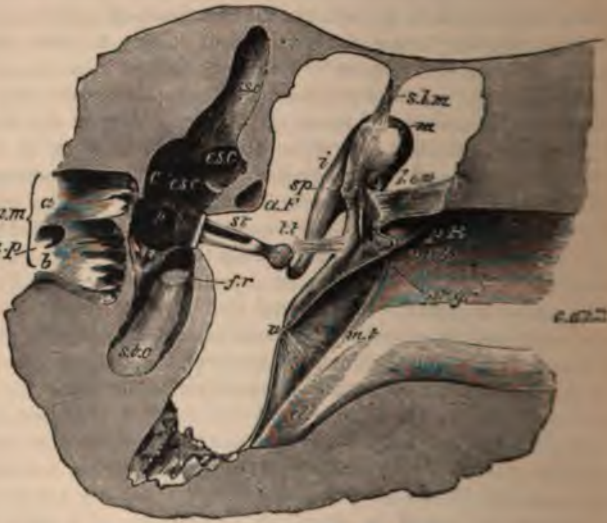


Fig. 234.—Diagram of the tympanum, showing the relation of the ossicles to the tympanic membrane and the internal ear. The tympanum is cut through nearly transversely, and the cavity viewed from the front (left ear). (Schäfer.)

m.t, Membrane of the drum to which the handle of the malleus is attached at *u*. *m*, head of malleus, which is held in position by its suspensory ligament *s.l.m*, and external ligament *l.e.m*; *i.*, long process of incus connecting malleus and *st.* stapes, the base of which closes oval opening of the vestibule. *e.au.m*, external auditory meatus. *i.au.m*, internal auditory meatus, where the two parts of the auditory nerve enter, *a* and *b*.

and no succession of vibrations follows the first effect of the sound waves.

The existence of any special note of its own is prevented by its conical shape, which is partly due to the traction of the handle of the malleus. If a stretched membrane, such as that of a drum, be drawn out at its centre so that it is no longer a flat surface, then its tension is different at the centre and the periphery, being, of course, greatest at the point at which it is drawn upon, and gradually decreasing towards the margin. Since the existence of a tone of a definite pitch depends upon a certain degree of tightness of the membrane, if no two parts of the membrane have exactly the same degree of tightness, then of course no one tone can be more conspicuous than another. This is the case with the tympanic membrane.

The independent vibrations of the membrane are further prevented by the tympanic ossicles. These little bones do not really vibrate, but move back and forwards in time to the sound-vibrations. If a body, not capable of vibrating with the membrane of a common drum, be attached to it, the drum would not sound. A touch of the finger of the musician to the membrane suffices to check the sound produced by a drum. The handle of the malleus, which is joined to the other bones, being fixed to the membrane, acts in this way as a damper, and checks the continuance of any special vibration in the membrane of the drum.

The small muscle attached to the malleus so as to draw it towards the cavity of the drum is called the tensor tympani.

CONDUCTION OF SOUND-VIBRATIONS THROUGH THE TYMPANUM.

The motions occurring in the membrane of the drum are conveyed across the tympanic cavity by means of the three small bones known as the malleus, the incus, and the stapes. Together, these ossicles form an angular or two-armed lever, one end of which (the handle of the malleus) is attached to the centre of the tympanic membrane, and the other (the long limb of the incus) which is the shorter arm of the lever, pushes the stapes against the little secondary tympanic membrane, which fits the oval opening leading into the vestibule. The stirrup bone acts as a kind of adaptable extremity to this inner arm of the lever, being adherent to the membrane of the vestibule and jointed to the long arm of the incus. This little angular lever works round an axis which passes from before backwards through the head of the malleus, and *lies above* the membrane of the drum. The two points which act as the bearings or pivots of the motion being the slender process of the malleus in front, and the short limb of the incus behind.

When the tympanic membrane vibrates in response to the sound waves of the air, it moves in and out, and the handle of the hammer bone must move in and out with it. The body of the incus, being fixed by a firm joint to the head of the malleus, must follow these movements, and thus they cause the little oval foot-piece of the stirrup to press in or to draw out the membrane which separates the tympanum from the vestibule. Thus the vibrations of the air communicated to the tympanic membrane are conveyed across the cavity of the drum to the liquid in the labyrinth.

A small muscle—the stapedius—is attached to the stapes near its junction with the incus, and pulls upon it in such a direction that the bone is drawn out of the line of motion. This action, possibly, has the effect of reducing the effect of the more ample vibrations of the tympanic membrane, which might have too great an effect upon the liquid in the labyrinth.

The tympanum is connected with the pharynx by means of the Eustachian tube which, though habitually closed, is opened for a moment by swallowing and other motions of the pharynx. On these occasions air can pass in or out of the tympanum easily, so that the pressure on the two sides of the membrane of the drum is equalised. When there is too much or too little air in the tympanic cavity, the tympanic movements are impeded. This difficulty is felt when one has a bad cold; the tube is occluded by the inflammatory swelling of the mucous membrane. Or when one performs what is known as Valsalva's experiment, *i.e.*, to hold the nose and violently puff air into it; when the tubes are blown open, too much air is often retained in the tympanum, so that the pressure from within is higher than that from without, and hearing becomes dull. If, now, the act of swallowing be performed, the feeling of tension leaves the ears and hearing becomes as acute as before.

The Eustachian tube also acts as a way of escape for any fluid that may be secreted by the epithelial lining of the tympanic cavity. This fluid is so minute, that the periodic opening of the tube suffices, under ordinary circumstances, for its complete escape. When increased by disease, however, it may collect in the tympanum and require catheterisation.

If the tube were permanently open, we should suffer from two great disadvantages. In the first place, at every breath, even during ordinary respiration, some little change in tension of the air contained in the cavity of the drum would occur and impair the hearing; and secondly, the vibrations of the air in the pharynx, produced by the voice, would enter the drum directly, and give rise to an exaggerated shouting noise.

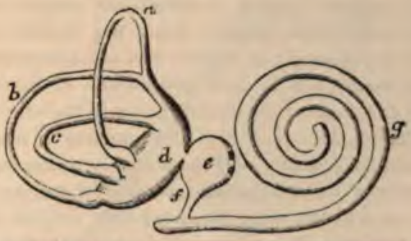


Fig. 235.—Diagram of the membranous labyrinth. *a*, *b*, *c*, **semicircular canals opening into the ventricle** *d*; *e*, **the saccule from which the uniting canal leads into the membranous canal of the cochlea,** *g*. **(Cleland.)**

CONDUCTION THROUGH THE LABYRINTH.

Every motion of the oval base of the little stirrup bone causes a wave to pass along the liquid in the labyrinth. The bony case of the internal ear being firm, and its contained liquid—like most liquids, quite incompressible—the wave travels through all the parts of the internal ear. Through the cochlea it can arrive at the yielding membrane covering in the round opening, which separates the cavities of the tympanum and the cochlea. To pass from the oval vestibular opening which is closed by the stapes, to the inner tympanic membrane which closes the scala tympani of the cochlea, the waves have a very complex route. From the liquid lying around the membranous labyrinth—the perilymph—the waves pass up the fluid in the vestibular spiral of the cochlea, and arriving at its summit, they descend by the tympanic spiral to the round opening. In this course they pass at first over and then under the fluid contained in the membranous canal of the cochlea—endolymph—in which the special nerve terminations of the cochlea are placed.

For the construction of the labyrinth the student is referred to the text-books of anatomy, as space only admits of a brief account of the special arrangements of the nerve-ending being given.

The nervous mechanisms which are most important for the appreciation of tones are those situated in the cochlea.

The endings of the nerves which are found in the membranous sacs in the vestibule are connected with peculiar epitheloid cells, to which are attached fine bristle-like processes. These processes lie in the *endolymph*, and are related to calcareous masses called *otoliths*. Waves in this endolymph possibly bring the otoliths into collision with the hairs, and thus give a stimulus to the nerve-endings. Thus noises may be heard, but no fine impressions of tones can be explained. The exact use of the nerves going to the other parts of the labyrinth—namely, the *ampullæ* of the *semicircular canals*—is somewhat doubtful, and possibly not immediately connected with hearing.* The coils of the snail-shell-like cochlea are throughout their entire length, even in the dried state, partially divided into two by a kind of shelf projecting from its central axis into the spiral cavity. This is called the *osseous spiral lamina*. In the fresh state the separation of the spiral canal into an upper (vestibular) and a lower (tympanic) coil is completed by a membranous partition, which stretches from the bony spiral lamina to the opposed side of the spiral canal. This is called the *membranous spiral lamina*, and forms the base upon which the special nerve-endings of the organ of hearing are spread out. An extremely delicate membrane called the *membrane of Reissner* stretches from the upper side of the spiral partition obliquely upwards to the outer wall of the spiral cavity, so as to cover the special organ, and shut off that part of the vestibular coil which lies over the membranous spiral lamina. This *canal of the cochlea* is triangular in section, and is separate from the rest of the spiral cavity. Its floor is made up chiefly of the membranous spiral lamina, particularly the part called the *basilar membrane*, while the oblique roof is composed of only the thin membrane of Reissner. This space follows the turns of the cochlea, lying between the vestibular coil and that leading to the tympanum, and it is filled with a fluid (endolymph) which is quite separate and distinct from that in the vestibular or tympanic coils of the cochlea (perilymph).

The cochlear division of the auditory nerve passes into little tunnels in the central bony column around which the coils of the cochlea turn, and it gives off a spiral series of branches which run through the osseous spiral lamina to reach the membranous portion. A collection of ganglion cells connected with the radiating nerve-fibres is found lying in a spiral canal in the osseous lamina. Passing through the bony spiral the nerves reach the basilar membrane, which, as before

---

* Compare equilibration, in connection with which they will be described, p. [illegible]

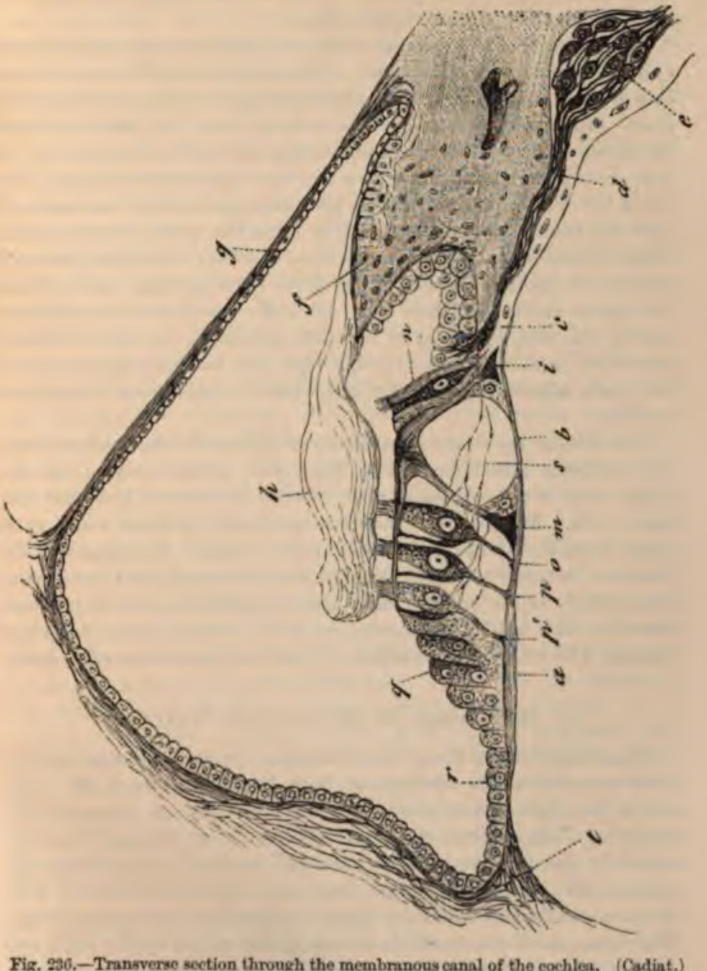


Fig. 236.—Transverse section through the membranous canal of the cochlea. (Cadiat.) *a*, Striated zone of basilar membrane; *b*, Pectinate zone of the basilar membrane; *c*, Perforated zone of basilar membrane through which the nerves pass; *d*, Nerve fibres from spiral ganglion; *e*, Spiral ganglion; *f*, Limbus; *g*, Reissner's membrane; *h*, Tectorial membrane; *i*, Internal rod of Corti; *m*, External rod of Corti; *o*, *p*, *p*, Special cells receiving nerve terminals; *q*, Epithelial cells covering the basilar membrane; *s*, Nerve fibres; *t*, Spiral ligament.

mentioned, forms a great part of the membranous spiral lamina, and upon which the organ of Corti is placed.

The *organ of Corti*, placed within the membranous canal of the cochlea, is made up of a series of peculiarly curved bars or fibres, called the rods of Corti, and some remarkable cells provided with short, bristle-like processes. The rods of Corti are fixed by their broad bases upon the basilar membrane, and unite above in such a way that the outer and inner rods together form a bow or arch. The spiral series of rods thus propped up against each other leave a small space or tunnel under them, which runs the entire length of the basilar membrane. Beside these rods of Corti are placed rows of cells of an epithelial type into which the nerve-endings pass. From the upper surface of these cells, on a level with the apex or junction of the rods, a number of hair-like processes project. A delicate *reticulated membrane* lies over the rods and the cells, and seems to be lightly attached to their surface, while the hairs pass through its meshes.

The *basilar membrane* is made up of fibrous bands held together by a delicate membrane. The fibres pass transversely across the spiral canal of the cochlea, so as to subtend the bases of the outer and inner rods. The basilar membrane gradually becomes wider as it passes from the base to the summit of the cochlea. The length of the rods also increases towards the summit of the organ, their bases being more widely separated from one another and their point of junction nearer to the basilar membrane, so as to form a lower and wider tunnel. The entire number of rods of Corti has been estimated at 3,000.

STIMULATION OF THE AUDITORY NERVE.

The stimulation of the nerve of hearing by sound-vibrations of the air is less difficult to understand than the excitation of the optic nerve by light-waves which are conveyed by an imponderable medium. The motions of the membrane of the drum, being conveyed in the manner already indicated to the liquids within the internal ear, pass first over and then under the cells connected with the nerve terminals, which are placed on the elastic basilar membrane. The *transverse* fibres are set *in motion* by the waves in the fluid, and as they vibrate they communicate the motion to the rods of Corti. The bases of the inner rods, being fixed at the inner margin of the basilar membrane, can move but little, and the bases of the outer rods being placed near the middle of the fibres of the membrane, where the motion of the vibrations is most extensive, a slight change in their relative positions, and a consequent movement of the apex of the bow, must take place. This movement at the apex of the bow, where the rods join, is communicated by the medium of the reticular membrane to the hairs in the special auditory cells, thence to the nerves, where an excitation is produced which gives rise to the transmission of an impulse to the brain.

But we can distinguish differences of (1) loudness, of (2) pitch, and of (3) quality in sounds.

Since the loudness depends simply on the amplitude of the vibration, we can have no difficulty in understanding how varieties in it can be appreciated, since the more ample the vibration the more marked the motion, and, therefore, the more intense the stimulation of the nerve terminals. What we call the loudness of a sound, then, simply means greater or less intensity of stimulation of the nerve.

The comprehension of the perception of differences of pitch presents greater difficulty. As already mentioned, this depends on the rate or period of vibrations. We know that most bodies capable of producing sound vibrations have a *proper tone*, *i.e.*, that which they produce when struck. When the proper tone of a body capable of vibrating is sounded in its immediate neighbourhood, this is also set vibrating through the medium of the air. If a clear tone be sung loudly over the strings of a piano a kind of sympathetic echo will be heard to come from the chords, on account of the strings corresponding to the notes sounded being thrown into sympathetic vibrations. Now, in the basilar membrane we have practically a series of strings of different length—since the membrane gets wider as it passes from below upwards to the summit of the cochlea—and therefore a great variety of proper tones. With a high note, then, a fibre of one part of the membrane will readily fall into vibration, and with a low note a fibre of another part. Different nerve fibrils are in relation to these different parts, and thus we may conclude that tones of different pitches stimulate distinct nerve-terminals, and are conveyed to the brain by separate nerve-channels. Impulses arriving at certain brain-cells then give rise to the idea of high tones, and impulses coming to others cause the impression of low tones. There are about a sufficient number of fibres in the basilar membrane for all the notes we can hear, viz., from about 30 to 4,000 waves in the second.

The rods of Corti cannot be the vibrating agents, because they are too few in number, and they are absent in birds, which appreciate and reproduce various notes. Further, the rods are not elastic, and therefore *not* well suited to vibrate. It may therefore be concluded that they only act as levers which convey the vibrations of the fibres of the basilar membrane to the nerve-endings in the auditory cells.

The explanation of our wonderful appreciation of the delicate shades of *quality* of tones is more difficult. Even persons with indifferently good ears, as musicians say, and no special musical education can at once distinguish between the quality of the same note when sounded on a violin, a piano, and a flute. In examining the resonance from a piano when a note is sung against its strings it becomes obvious that with ever so pure a tone a great number of strings are set vibrating. It will be found that not only the string which sounds the note vibrates, but also all those strings that have a certain simple numerical relation to its number of vibrations. In fact, all its over-tones or harmonics are also sounded. Now, in the cochlea we suppose the same takes place with the fibres of the basilar membrane. Not only does the one fibre whose proper tone is sounded vibrate in response, but also all those fibres which represent the many and varied over-tones or harmonics of the fundamental tone that reach the ear. It has already been pointed out that *quality* of a note depends on the relative number, force, and arrangement of the harmonics which invariably accompany any musical note possessing a definite character.

When such a note, then, arrives at the auditory nerve-terminals, one of these is strongly stimulated by the wave of the fundamental tone, and many others are stimulated by the different over-tones. Thus, a complexity of impulses, corresponding to a mixture of tones of varying intricacy, is transmitted to the brain-cells, where it gives rise to the impression of the quality which we by experience associate with that of a violin, flute, or piano, as the case may be.

With regard to the judgment of the distance of sounds, it need only be remarked that they chiefly depend on former experience of the habitual quality and intensity of the sounds. A faint sound with the same quality that we familiarly attribute to loud sounds seems to us to be far away. Thus, sounds reaching our labyrinths by the cranial bones appear distant, and ventriloquists deceive us by imitating the character of distant sounds.

In man the direction from which sounds come is chiefly judged by the difference of distinctness with which they are heard by one or other ear. When we cannot form any idea of whence a sound comes we usually turn our heads one way or the other in order to present one ear more directly to the origin of the sound. When a sound is either directly behind or before us we cannot judge which position it really comes from, unless the head be slightly turned to one side or to the other.

CHAPTER XXXIV.

CENTRAL NERVOUS ORGANS.

THE more important properties of the peripheral nerves and their terminals have been discussed in the previous pages. The central part of the nervous system, which remains to be considered, consists of the spinal marrow and the brain. These parts are composed of a soft texture, the elements of which are held together by a peculiar and very delicate form of connective tissue, known as *Neuroglia.* With the naked eye the central nervous organs can be seen to be made up of two distinct kinds of substance: (1) a white substance, which is found by the microscope to be composed of nerve fibres, with a medullary sheath, and (2) a grey substance, consisting of a dense feltwork of naked axis cylinders, with numerous ganglion cells interspersed between them in various quantities and relationships.

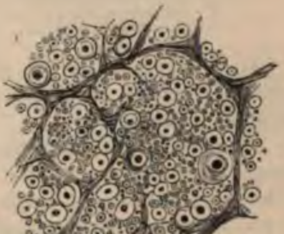


Fig. 237.—Transverse section of nerve fibres, showing the axis cylinders cut across, and looking like dots surrounded by a clear zone, which is the medullary sheath. Fine connective tissue separates the fibres into bundles.

In the brain the grey substance is distributed chiefly on the surface, forming a kind of grey cortex, which follows all the irregularities of the convolutions. In the spinal cord the grey matter is situated inside, and the white outside. The grey substance of the cord forms separate columns on either side, which run its entire length; but is thicker in the cervical and lumbar regions. These grey columns, together with their connection with the roots of the spinal nerves, divide the white substance of the cord into separate columns.

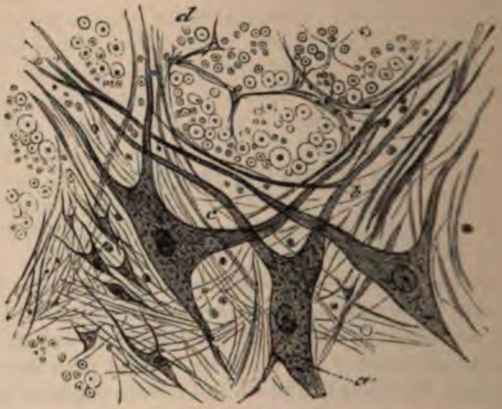


Fig. 238.—Multipolar cells from the anterior grey column of the spinal cord of the dog-fish (*a*) lying in a texture of fibrils; (*b*) prolongation from cells; (*c*) nerve-fibres cut across. (Cadiat.)

As already pointed out, the nerve fibres are simply conducting channels for the transmission of nerve impulses from one cell or terminal to another.

The nerve or ganglion cells are remarkable for their large size, their large clear nucleus, distinct nucleolus, and fibrillated protoplasm. They have, at least, one—more commonly several—processes connected with them, and are commonly called uni-, bi-, or multi-polar cells. Often one of these processes is more distinct and more definite than the others, and does not sub-divide into branches like them. It appears to be connected directly with the axis cylinder of a medullated nerve fibre.

The nerve-cells can conduct the nerve impulses which reach them by any of their attached poles, and they can transmit these impulses on to other cells by means of their protoplasmic strands of intercommunication. They thus frequently seem to direct an impulse coming by a sensory or afferent nerve from the surface back again by an efferent nerve to some texture or organ in the neighbourhood. Thus, the slightest stimulation of the conjunctiva causes immediate and involuntary winking of the eyelid. This kind of transmission of an impulse in a direction differing from that by which it arrived at the nerve-cell is called reflexion, and motions such as that just alluded are called reflex acts. Collections of cells, whose duty seems to be habitually to receive impulses from the periphery and to change their direction, are called reflex centres.

Some groups of nerve-cells send forth impulses, either constantly or periodically, without receiving any nerve impulse from the surface. Such centres are called *automatic* since they appear to act independently of influences from without. The only source of energy these cells have is the warmth and nutrient material carried to them by the blood flowing in their immediate neighbourhood. The vaso-motor centres are good examples of automatic centres, in which the constant or tonic character of action predominates. The respiratory centre is one from which automatic impulses are rhythmically discharged by a special regulating apparatus.

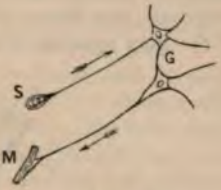


Fig. 239.

S. Sensory receiving organ with attached afferent nerve fibre.
G. Central organs—ganglion cells.
M. Peripheral organ and efferent nerve.

Besides having the power of *conducting*, *reflecting*, and *originating* impulses, we must attribute to the activity of the nerve-cells of the brain the various mental phenomena, such as feeling, thought, volition, memory, &c., which form of activity may be excited either by impulses arriving from without, or from the spontaneous (automatic) action of the cells of the cerebral cortex.

THE SPINAL CORD.

Being the great bond of connection between the brain and the majority of the peripheral nerves, the spinal cord is obviously a *conducting* apparatus of the very first importance, and from the quantity of nerve-cells lying in its grey matter, it must also enjoy the function of a governing organ or nerve *centre*.

These two great duties of the spinal marrow had better be considered separately :—

I.—SPINAL CORD AS A CONDUCTOR.

From the anatomical investigation it may be seen that there must be some special method of conducting impulses along the spinal marrow, and that it is not merely a collection of the nerves or an

aggregation of the fibres that spring from it. In the first pla
these nerves, if all bundled together, would be much larger than th
cord, even at its thickest part; and, further, it does not taper even
towards its lower extremity, as it should were each succeeding pa
of roots a direct loss to its thickness.

The posterior roots of the spinal nerves pass through the white sub
stance to reach the posterior grey column, where they break up int
numerous fine twigs, which are distributed to neighbouring par
of the grey network of fibrils, in which they are lost without the

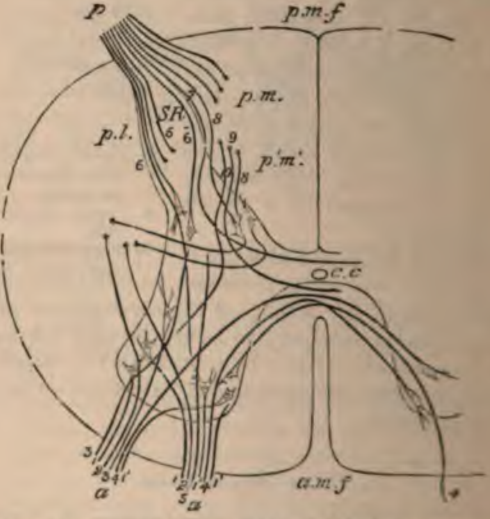


Fig. 240.—Diagram illustrating the course probably taken by the fibres of the ner
roots on entering the spinal cord. (Schäfer.)
a.m.f., Anterior median fissure; *p.m.f.*, Posterior median fissure; *c.c.*, Cen
canal; *s.r.*, Substantia gelatinosa of Rolando; *a.a.*, Funiculi of anterior ro
a nerve; *p.*, Funiculus of posterior root of a nerve. By following the fi
1, 2, 3, &c., their course through the grey matter of the spinal cord may be tra

union with the cells being obvious or immediate. The fibres
anterior roots traverse the superficial white part of the cord
their way to reach the anterior grey columns, into the cells of whi
they can be directly traced. The numerous processes from the
cells then pass into the fibrillar network which lies between th
cells and makes up the great mass of the grey substance. By mea
of two sets of fibres (one lying in the lateral white column, on th

same side, and another, which crosses at once to the other side of the cord) these cells are kept in communication with the parts of the cord above. The medullated nerve-fibres of the cord then are not directly continuous with those of the roots of the spinal nerves, but seem only to have the function of connecting the different regions or districts of the cord with one another, and with the brain, and they thus establish a near relation between the cells in the lumbar, dorsal and cervical regions of the spinal cord, with the medulla oblongata, &c.

Histology thus leads us to expect that the essential parts of the cord are—(1) innumerable fibrils in the grey matter, and (2) series of groups of cells all intimately connected with one another, with the cells in the masses of grey matter at the base of the brain (cerebellum), and with the fibres in the anterior and posterior spinal roots, by which they are related to sporadic ganglia and the various tissues and organs. The white fibres of the cord are then, probably, only used for the more rapid conveyance of impulses from one group of cells to some others lying in a distant region of the cord itself, while the main conducting work is accomplished by the fibrils of the grey matter.

Experiments have taught us the following facts :—1. Section of the cord causes loss of both sensation and motion in the part *behind*—speaking of a lower animal—the point of section (Galen). 2. Section of one side of the cord is followed by loss of sensation on the same side with increased sensitiveness and loss of motion (recovering slowly) on the side opposite to the injury. 3. Division of the cord in the median line gives rise to impairment of feeling in a badly-defined part of the surface, but no loss of motion. 4. Section of the posterior white columns gives rise to the loss of perception of tactile, temperature, and muscle sense, but the sensation of pain can still be felt. A partial section of these columns is followed by a local loss of touch in a part of the skin of corresponding extent. This lesion is complete, as if the impulses were transmitted directly by definite fibres in the cord from each region of the skin. 5. Section of the antero-lateral white columns causes loss of voluntary power in a corresponding part of the same side of the body. If the grey matter be perfect, the power of motion is soon restored, showing that the grey matter can take on a function habitually performed by the medullated fibres. The respiratory and vaso-motor impulses appear to be conveyed in the lateral white columns. 6. If the grey matter and the posterior white columns be quite cut across, the impulses giving rise in the brain to common *sensation (pain)*, as well as tactile impulses, are no longer carried to the centres, which shows that the impulses causing common sensation travel exclusively in the grey substance. 7. Section of one side of the grey matter has, however, little effect. The passage of painful impressions is not quite lost, even if both sides be cut at different regions of the cord. The dulness of feeling is moreover *general* below the injury; no one spot of skin being quite anæsthetic. A kind of delay in transmission occurring from the "blocks," as if constant decussation of the fibrils exists, but no direct or special channels of communication. If the posterior white column be left intact, the skin may transmit tactile impulses, but not painful ones. This remarkable condition, called "analgesia," sometimes occurs in the human being when partially under the influence of chloroform.

THE SPINAL CORD AS A COLLECTION OF NERVE CENTRES.

The various groups of cells in the spinal cord are in more or less direct union with the roots of the nerves, and the conducting fibrils of the cord itself, so that they participate in the transmission of the impulses to and from the centres situated in the brain. In the transmission of these impulses the cells seem to have a certain directing and controlling influence which deserves special attention, as it gives us the key to the more complex mechanisms of the higher centres. Although the various powers exerted by the cells of the spinal cord are so intimately associated together as to be practically inseparable, it is found convenient to consider their functions under distinct headings. The following division of their duties will be found useful in working out their general function, viz.:

1. Their influence on afferent impulses.
2. Their influence over efferent impulses.
3. Their automatic or independent power of originating impulses.

When an impulse—the result of some slight stimulus, such as the prick of a pin—arrives at the cells of the spinal cord, it is at once communicated to the other cells in the immediate neighbourhood, and reaching some cells connected with motor nerves it gives rise to a movement of the muscles of the neighbourhood from which the impulse first started. At the same time impulses travel to the brain and there give rise to a consciousness of the various events taking place, *i.e.*, a local stimulation and a local movement. The action of the cells of the cord takes place without the aid of the will, and generally occurs before one is conscious of it; it is therefore called an involuntary act, and on account of being a throwing back of the impulse, these kind of movements are called *reflex acts.*

Reflex action forms one of the commonest duties of the cells of the spinal cord. Even the gentlest stimulation commonly gives rise

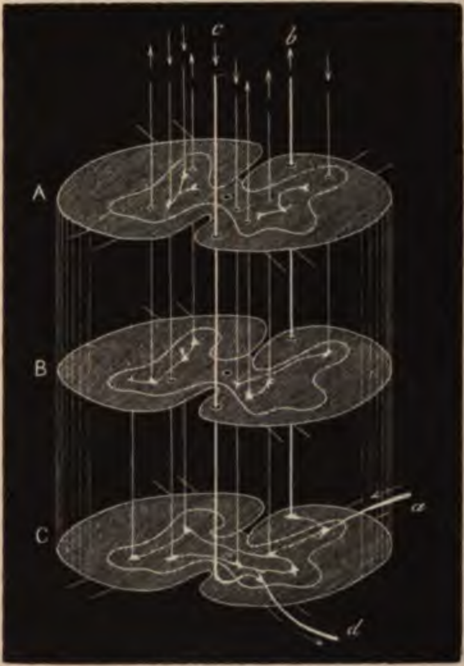


Fig. 241.—Diagram illustrating the course taken by the fibres in the spinal cord. (After Fick.)

A, B, and C represent oblique views of three transverse sections of the cord, the tissue between which is supposed to be transparent. The outline of the grey substance is marked with a line, which encloses the ganglion cells. At the lowest section (C), sensory nerve fibres (*a*) enter by the posterior root, and after connection with ganglion cells of the grey matter, communicate with the posterior white column, through which some passes directly to the brain, as shown by the direction of the arrow-head pointing to (*b*). This is the route which offers least resistance to an impulse travelling to the brain through the cord. Hence it is that traversed by weak peripheral (tactile) stimuli.

By the same posterior root arrive impulses at the cord which may traverse the finer, more irregular and resistant fibrils of the grey matter—shown by the fine lines. Through these channels painful sensations are carried.

From many parts of the grey matter of the cord ganglion cells may dispatch impulses by the motor root (*d*). Hence many reflex actions are arranged. When an impulse comes directly from the brain (voluntary centres) it adopts the direct route (*c*), which passes through the white substance of the anterior columns, *before it excites* the motor ganglion cells of the cord to co-ordinated activity.

definite and familiar action is performed. For exam
burning head of a match adhere under the thumb-nai
a mere withdrawal of the hand takes place. The e
violently shaken with the obvious purpose of shaking off
stimulus before the will has time to come into oper
then, we have a complex form of *co-ordination* of purpose
movement, as the immediate result of an impulse com
skin, and this co-ordination is the result of mutual relati
ing between the cells of the cord employed in trans
sensory and motor impulses. Not only is the movem
and co-ordinated act, but in many cases, as has just bee
it is performed with a definite purpose, as if it were
thought, but since there need be no consciousness it cann
All these points may be easily studied on a frog, kill
hour beforehand by decapitation. If a fragment of bl
moistened in weak acid, be placed on the skin of the bo
animal, in a position not easily reached by the foot, a n
series of movements follows first with one leg then the o
both. The muscular action is both elaborately co-ordina
poseful; indeed, the movements of the headless anim
called ingenious, and usually result in the removal of
paper.

If the degree of the stimulation be carefully regulat
found that the results obtained by peripheral stimulatio
(*a*) the strength of the stimulus, and the length of time

body. If the stimulus be further strengthened, the movements become violent and more extended until the whole body is tossed about by co-ordinated motions. The movements seem to spread from the local nerve cells to their neighbours, and then to reach those governing the corresponding muscles of the other side, in which, however, they are always less marked than in those of the side stimulated. This spreading of movement from one set of muscles to another, as the strength of the stimulus is increased, of course, must be preceded by a spreading of the impulse from one group of nerve-cells in the cord to another by a kind of radiation from the focus of excitation.

Very slight stimulation, though not sufficient to produce immediate response, may, after a time, give rise to definite reflex action, as if the weak impulses arriving at the nerve-cells in the cord were stored up until their sum sufficed to produce a definite reflex movement. This may also—indeed, much better—be seen in animals whose nerve centres are intact, for the cells of more remote parts exercise a kind of checking influence on those in the region receiving the stimulus, and thus the accumulative action (summation) comes more commonly and more effectively into play. This is seen in the human subject where slight visceral stimulations exist for a long time. In some of these cases, even without any really sensory appreciation of any local excitation, an amount of energy may be accumulated along the grey tract of the cord from the prolonged income of impulses, that will bring on the most extensive forms of reflex muscular movement, and give rise to serious results. These movements are generally different from the regular co-ordinated motion resulting at once from an adequate skin stimulation, and have usually a tendency to assume a convulsive form. As an example of this may be named the convulsions that commonly occur in young children, from the prolonged irritation of intestinal worms, or during the painful period of dentition. Epilepsy and hydrophobia may possibly be explained in the same way.

In certain conditions of the nervous system these irregular movements or spasms (convulsions) can be excited much more readily than is normally the case. As most striking among these, may be named poisoning with the alkaloid of nux vomica (strychnia) and the state of the blood which is produced by cessation of the respiratory function (asphyxia). These toxic conditions of the blood bring about a peculiar excitable condition of the cells or conducting fibres of the spinal cord, in which impulses seem to pass with unwonted facility from one part to another, and give rise to an excessive degree of action even in response to normal stimulations. A frog poisoned with strychnia is thrown into general spasm of the entire body by even the least touch, which normally would only cause it to withdraw the limb slowly.

On the other hand, there are many poisons which seem to have the effect of dulling the reflex powers of the cord centres, among these are opium, chloroform, chloral, digitalin, &c. And the condition of the blood which may be brought about by too rapid respiratory movements (apnœa), has also the effect of lowering the excitability of the spinal nerve cells, and slowing respiration.

The great majority of reflex actions may be prevented or controlled by the will, and the masses of cells in the basal ganglia and medulla seem habitually to exert a checking or inhibitory action on the reflex actions of the spinal cord. It is in this way that we account for the well-known facts that in a frog which has not been decapitated it is impossible to induce the ordinary regular reflex movements, and that a human being, when asleep, shows well marked reflex action in response to a slight stimulus that would be quite ineffectual when he is awake. We know, too, that for some little time after pithing a frog one cannot count on constant or regular results, because the act of section of the upper part of the spinal cord acts as a stimulus to those channels which habitually bear impulses from the brain, and, by exciting them, has the same inhibitory effect. Further, it has been said that artificial stimulation of the corpora-quadrigemina and medulla have the effect of completely checking the reflex action of the cord.

It is not only impulses coming from the higher centres that are capable of inhibiting reflex activity. If, while the cord is employed in reflex action, in response to gentle cutaneous stimulation, a large sensory nerve trunk be stimulated with an interrupted electric current, the reflex action ceases. In short, it may be accepted that strong impulses arriving at the cord from any direction, have the effect of inhibiting the action of its reflecting cells.

The theory of reflex action lies at the bottom of all nervous activities, and it is therefore useful to attempt to work out the details of the mechanisms by means of which it is carried on. The simplest scheme of the channels traversed by the impulses is given in the diagram (Fig. 241), in which the arrow-heads show the direction of the afferent impulse passing along the posterior root of the cord to reach the cell in the posterior grey column, thence through the fine grey network, it passes to a cell in the anterior column, to reach the efferent fibre, and through the anterior motor root of the nerve on its way to the muscle. It has been suggested that the impulse meets with siderable resistance in passing through the protoplasm of the cells, and that owing to this resistance the effect of a slight stimulus remains localized, while a more powerful irritation gives rise to impulses that can overcome the resistance, and thus spread to a greater number of cells, even reaching those situated in a remote district. *Thus the* co-ordination in the cord would be simply depend-

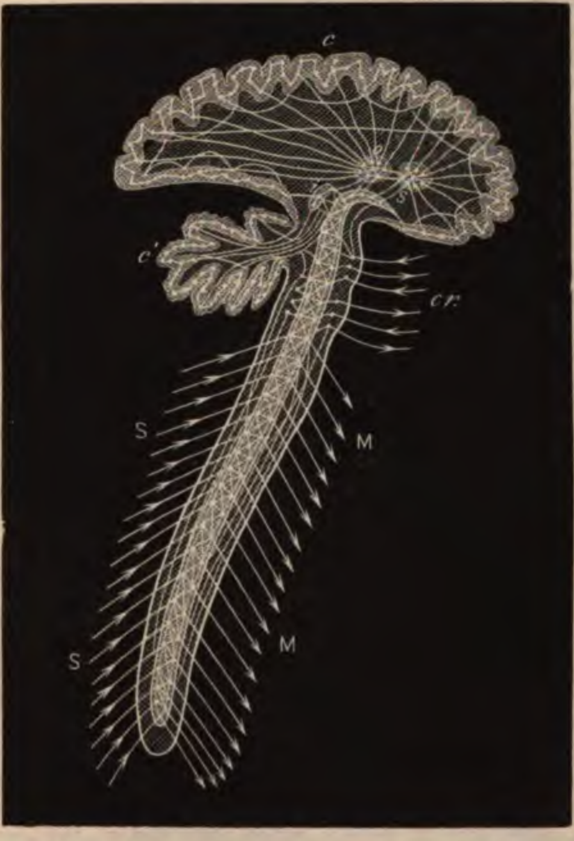


Fig. 242.—Diagram of the paths taken by the impulses in the brain and cord. MM., motor channels; SS., sensory channels; CR., cranial nerves.

ent on the inability of the impulses to affect cells other than those in their immediate neighbourhood, and the relation between the strength of stimulus and the effect would in this manner be easy of explanation. It has also been suggested that this resistance is increased by impulses arriving at the cells from a different direction, and the checking or inhibitory action of the higher centres, or intense peripheral excitation of another part, impedes the spreading of the impulses to be reflected and a lesser result is obtained.

But this view of *resistance* to and *interference* with the transmission of impulses in the nerve cells hardly explains all the phenomena observed even in the reflex action of the spinal cord and the various modifications it can undergo with varying conditions. It will, however, help us in formulating the mechanism if we suppose the resistance in the grey part of the nerve centres to be much greater than in the ordinary nerve channels, and that throughout it the ways are so infinitely numerous that we can imagine every individual nerve-cell to be in communication with every other nerve-cell by some path possible of being traversed. But these paths have to be made possible by use; the oftener an impulse traverses a given route the more adapted such a route becomes for future traffic. Thus, by practice or the habit of using certain sets of muscles, we constantly freshen certain channels of intercommunication between the various cells of the cord and thus make beaten tracks, along which impulses can pass without hindrance. The nerve-paths, along which the impulses, producing certain movements commonly performed by every individual, have to pass, are no doubt prepared by the long practice of our ancestors, and the power of performing these actions is transmitted to us ready for immediate application. Other paths required for the production of unusual combinations of movements have to be worked out by the individual, and much of the difficulty of learning any trade depends on the necessity of making impulses readily traverse some definite directions, so as to excite certain groups of cells to act synchronously and set certain sets of muscles in accurately co-ordinated motion. Indeed, the delicacy of manipulation required by some trades cannot be attained in the lifetime of one individual; thus, it is said to take three generations to make a perfect glass-blower; the grandson having the benefit of the hereditary tendency to accomplish certain co-ordinations acquired by the life-long habit of the parents.

The reflex convulsions that occur in poisoning with strychnia, or as the result of some constant but slight stimulation, may be explained as follows:

We know that, besides the resistant thin paths of connection between the cells of the cord, there also exist medullated fibres—short cuts, as it were—for impulses to travel from one part of the cord to another, for the various cell groups are in communication with those situated in the other regions, by means of fibres that lie in the white columns. Now, if we suppose the ordinary reflex traffic of the cord-cells to be carried on without the assistance of these direct lines of communication, we must assume that there is some special means of shutting these fibres out of the working of the reflex machine. Such special mechanisms do, in all probability, exist, and are in relationship with, or under the command of the inhibitory cells of the higher centres. We may then suppose that strychnia removes the power of these special agents, and the impulses finding the direct ways from one part of the cord to another open, take these routes, and are simultaneously and irregularly diffused throughout all the cell territories (independent of the ordinary paths they have been educated to follow), and thus convulsive movements are excited in many parts of the body.

In like manner we can imagine that the unremitting activity necessary to keep in check the impulses arriving from a constant source of stimulation, such as intestinal worms, eventually fatigues the active elements in this inhibitory mechanism, and then—often suddenly—the force of the accumulated irritation, no longer restrained by the checking influence, rushes along the direct channels to all parts of the cord, and simultaneously exciting them brings many discordant muscles into spasmodic action.

The reflexion of an impulse from a sensory nerve, through the cells of the spinal cord to a motor nerve, occupies a measurable length of time, which has been estimated at about $\frac{1}{10}$ of a second. The time required for the performance of a reflex act varies considerably in the same individual under different conditions; of these, high temperature and intense stimulation shorten the time, and fatigue or cold lengthen it.

SPECIAL REFLEX CENTRES.

Many of the groups of nerve-cells in the cord are employed in executing definite familiar acts essential to the animal economy and more or less independent of the will. Many of these acts are very complex, and require the co-ordinated action of certain sets of muscles and the inactivity of others. Such groups of nerve-cells have been called special centres, and many of them have already been referred to in the preceding chapters, where a fuller consideration of them may be found. The more important are :

1. A centre for securing the retention of the urine by the tonic contraction of the sphincter muscle of the bladder. This group of nerve-cells is probably kept in action by impulses arriving from the bladder by the afferent nerves, passing from its walls to the spinal cord. The more distended the bladder becomes, the more powerful the stimulus sent to the cord, and therefore the more firmly the sphincter is made to contract.

2. Nearly related to the former is the centre which presides over the evacuation of the bladder. This is excited by impulses arriving from the urethra, near the neck of the bladder. It then sets the detrusor muscle in action, while the sphincter is relaxed by voluntary inhibition.

3. The ejaculation of the semen may also be said to be accomplished by a special spinal centre, capable of controlling certain special movements, in which involuntary muscles play an important part.

4. In parturition a number of motions are called into play (as well as the uterine contraction) which are so regularly co-ordinated as to entitle us to suppose that they are arranged by a special centre in the spinal cord.

5. The act of defæcation is accomplished by means of a spinal centre also. The action of this centre might (like that presiding over the urinary bladder) be divided into two parts—retention and evacuation—in which volition and intestinal peristalsis play a very important part.

AUTOMATISM.

Besides being excited to action by impulses coming from the brain—*volition*—and from the surface—*reflexion*—the groups of cells in the spinal cord may act without any obvious incoming impulse ; that is to say, some of the cells are capable of spontaneous activity. Such groups of nerve-cells are commonly called automatic centres ; the more important of those found in mammalia may be classified as follows :

1. Vaso-motor centres : Though the central point from which the contractions of the blood vessels is controlled is situated in the medulla, there is no doubt that even in mammalia centres are distributed throughout the grey matter of the spinal marrow, which are capable of keeping up the arterial tone in the regions to which they correspond. As evidence of this may be mentioned the fact that the dilatation of the arteries, which follows the severance of the lumbar part of the cord from the medulla, only lasts a few days, after which the vessels again contract in the usual tonic

manner. The arterial tonus only disappears completely and permanently when the spinal cord is destroyed. Thus, it would appear—although habitually the vessels of all the body are regulated by a centre in the medulla, nearly related to the cardiac centre—that every vascular region has a nervous mechanism of its own in the cord, which suffices to keep up the tonic contraction of the muscular coat of its vessels as soon as the necessary new lines of intercommunication have been opened between the different districts most nearly related to it.

2. Sweating centres: Though closely related to the preceding, the centres which preside over the secretion of sweat in the lower part of the body and hinder extremities must, for many reasons which cannot now be mentioned, be regarded as separate centres.

3. Many sets of smooth muscle-fibres appear to be kept in a state of tonic (automatic) contraction by means of centres in the cord. Thus, in the lower part of the cervical cord is a group of nerve-cells which keep the dilator muscle of the iris partially contracted; a narrowing of the pupil has been described as following injury of this region.

4. The grey matter of the cord is also said to keep the skeletal muscles in a state of slight tonic contraction, either from automatic or reflex stimulation.

On account of the elaborate and purposeful reflex movements performed by decapitated frogs or eels, it has been suggested that in the lower vertebrates the spinal cord is capable of sensation and volition—mental activity—but to follow this assumption, we should have to modify our ideas of volition and sensation, for which consciousness is commonly taken to be a necessary factor. It is, however, important to note that the lower we come in the scale of vertebrate animals the less powerful are the mental faculties, and the more important are the functions that the spinal marrow presides over.

CHAPTER XXXV.

THE MEDULLA OBLONGATA.

THE "oblong marrow" is the direct continuation of the spinal marrow, and contains the different items in the construction of the latter, prolonged upwards and mingled with some additional grey masses. The exact relationship of the different parts of the medulla to those of the spinal cord may be best understood if we suppose the latter, when it reaches its upper limit, to be split vertically on its posterior side down to the central canal, and the lateral masses so separated from one another that the central grey part of the spinal cord becomes spread out on the posterior surface of the medulla oblongata. The grey matter of the medulla oblongata consists, then, of two portions distinct from each other; one being the direct continuation of the grey columns of the spinal marrow, and the other being made up of certain grey nodules embedded here and there among the white strands. These latter, as a rule, subserve special functions, while the continuation of the grey columns of the spinal cord, which are spread out on the floor of the fourth ventricle, contains the nerve cells that preside over the movements which are most important for the every-day business of life.

The functions of the medulla may be conveniently divided, in the same manner as those of the cord, into its conducting power and its use as a central nervous organ.

THE MEDULLA OBLONGATA AS A CONDUCTOR.

The various white columns of the spinal cord are so distributed in the medulla that the anatomy of their course gives some indication of the channels by which impulses are carried through it. But here, as in the spinal cord, we should remember that the white fibres must be regarded as the direct and rapid means of transit of impulses, while the felt-work of fine fibres in the grey part can also conduct impulses in all directions. Though the readiness of transit is much less along the thin-fibred network than *viâ* the direct medullated routes, the complexity of paths and the variety of directions in which they lead, is much greater in the grey than the white substance. It is by means of the grey substance that the two lateral parts of the medulla are so nearly related to one another, and the local centres are kept in communication with the distant parts.

The posterior grey columns of the spinal cord are partly continued on by fine strands into the cerebellum by its peduncles, and partly are carried on to the brain through the cerebral peduncles. The antero-lateral columns are also distributed in part through the pyramids and peduncles to the cerebrum, and in part by the restiform bodies and peduncles to the cerebellum. In the pyramids the decussation of the anterior columns takes place, and it is believed that this is the point at which the direct channels carrying voluntary motor impulses to the skeletal muscles pass across from one side of the body to the other.

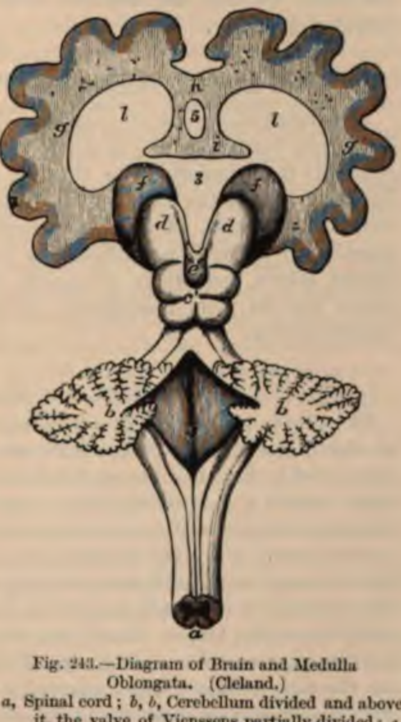


Fig. 243.—Diagram of Brain and Medulla Oblongata. (Cleland.)

a, Spinal cord; *b*, *b*, Cerebellum divided and above it, the valve of Vienssens partially divided; *c*, Corpora quadrigemina; *d*, *d*, Optic thalami; *e*, pineal body; *f*, *f*, Corpora striata; *g*, *g*, Cerebral hemispheres in section; *h*, Corpus callosum; *i*, Fornix; *l*, *l*, Lateral ventricles; 3, Third ventricle; 4, Fourth ventricle; 5, Fifth ventricle, bounded on each side by septum lucidum.

It must always be remembered that the medulla is the only route between *the brain* and the spinal cord, and in it some medullated channels cross and separate to pass to their cerebral connections, and the grey part of the spinal marrow is spread out on the floor of the fourth ventricle, and amplified by the addition of several separate foci of grey matter.

The Medulla Oblongata as a Central Organ.

A number of groups of ganglion cells with special and specific duties are located in the medulla; indeed, those acts which are obviously most important for the due execution of the vegetative functions, are, for the most part, arranged and governed by the nerve cells of the medulla. Some of these centres may be called automatic, though they are variously affected by many impulses arriving from distant points, and others are purely reflex in their action. The former are the more immediately essential, and will therefore be considered first.

Respiratory Centre.

The centre which regulates the motions of breathing has been known to be situated in the floor of the fourth ventricle at the upper and back part of the medulla ever since Flourens showed that injury of this spot—the vital point—was followed by almost instant cessation of respiratory movements and death.

This centre is a good example of a so-called automatic centre; that is to say, the blood flowing through the medulla and nourishing the cells suffices to supply them with the necessary energy for their periodic activity, and we know that the quality of the blood reaching this part modifies the activity of the cells; for the less oxygen and the more carbonic acid contained in the blood, the more powerfully does it act as a stimulant to the centre.

Although we take the respiratory centre as an example of an automatic centre, its daily work is arranged by means of afferent impulses, so that the normal rhythm of breathing is regulated and maintained by reflex action. The mechanical states of the lungs—whether distended as in inspiration or contracted as in expiration—seem to excite the terminals of certain fibres of the vagus, which carry impulses to the centre, and thus excite or restrain the inspiratory movements.

But this automatic centre can also be influenced by the higher centres of the brain, for by our will we can obviously regulate our breathing movements or stop breathing altogether for a time. And further, the action of the respiratory centre can be much altered by impulses arriving from the surface, as may be seen by the gasping inspirations which involuntarily follow the sudden application of cold to the surface.

Again, the activity of the centre may be quite altered by stimulations of certain parts of the air-passages ; so much so, that convulsive actions of the respiratory muscles are brought about, which induced some to speak of a *sneezing centre* and a *coughing centre* in the medulla. But sneezing and coughing may be equally well explained as a peculiar form of activity of the respiratory centre, or a reflex alteration in the respiratory rhythm, caused by irritation of the nasal or laryngeal mucous membranes, as by supposing that special reflex centres exist for the purpose of sneezing or coughing.

Though the action of the respiratory centre can be modified by (1) the will and by (2) various peripheral stimulations, and is habitually regulated from the periphery through the (3) vagi by the state of the lungs, the condition of the blood supplied to the centre may be such that these remoter influences may become quite powerless. This uncontrollable condition of the centre is established when the blood flowing through it is abnormally venous and the cells become over-stimulated. We all know how short a time we can hold our breath by voluntary checking of the centre, and most people have had occasion to observe the inordinate and painful efforts of a person whose respiration is interfered with by disease. When the dyspnœa becomes intense, nearly all the muscles in the body are called into action. Thus, in quiet breathing comparatively few nerve cells in the medulla carry on the work of respiration, but under certain emergencies they can call to their aid the entire motor areas of the grey substance of the spinal cord, and thus give rise to a kind of general effort. Hence we often hear of a *convulsive centre* in the medulla being placed in close relation to the respiratory centre. In cases, namely, irritation of the air passages or imperfect oxidation of the blood, the convulsive centre comes under the command of the cells of the respiratory centre, which can then excite coughing, sneezing, or convulsive inspiratory effort.

As already mentioned, the convulsion of asphyxia may also, in part at least, be explained by the impure blood acting as a stimulus to the cells of the cord itself.

THE VASO-MOTOR CENTRE.

It has already been stated that groups of cells exist in the grey part of the spinal cord, which, according to the class of animal, have *more or less direct* influence upon the muscles in the coats of the vessels. Thus in a frog, whose brain and medulla have been destroyed, in some hours the vessels of the web regain a considerable degree of constriction, which is again lost if the cord be destroyed. In the dog the vessels of the hinder limb also recover their tone more or less perfectly in a few days after the spinal marrow has been cut in the dorsal region, although just after the section they are widely dilated from the paralysis of their muscular coats. In a few days, then, the cells of the cord can learn to accomplish, of their own accord, work which they had been in the habit of doing, only under the direction of the higher centre. From this we conclude that though the cord contains local vaso-motor centres distributed throughout its grey matter, these are all under the direction and control of the vaso-motor centre in the medulla, and this centre is really the chief station from which impulses destined to affect the whole organism must emanate.

This arrangement is quite comparable with that by which the ordinary muscles are made to contract. When the will causes a muscular contraction, the impulse starting from the cerebral cortex does not travel directly to the muscle, but it passes from the brain to certain cells in the cord and thence to the muscles. In fact, to these spinal agents the ultimate arrangement and co-ordination of the act is confided. So, also, the chief vaso-motor centre in the medulla executes its orders through the medium of numerous under centres placed at various stations along the cord.

The vaso-motor centres—like nearly all other controlling groups of ganglion cells—must be considered to be made up of two parts antagonistic one to the other, viz., a *constricting* and *dilating* centre, the impulses from which commonly travel along separate nerve channels. The constricting impulses are mainly distributed by the sympathetic nerve, while the dilating impulses generally run in the ordinary peripheral nerves, which are employed in calling forth the ordinary function of the part in question. This is chiefly true of the internal organs, but in the limbs all the nerve channels are commonly collected together to form a single nerve.

From what has been said as to the wide distribution of centres influencing the blood vessels, an attempt to localise exactly the position of the medullary vaso-motor cells is not satisfactory. In the lower animals—frogs—the cells are evenly diffused throughout medulla and cord. In man the localisation is difficult to demonstrate, though we have reasons for thinking it much more definitely circumscribed than in the lower animals. In the rabbit it has been tolerably accurately localised to the floor of the fourth ventricle, in the immediate neighbourhood of the respiratory and cardiac centres. From this the nerves pass into the cord to the spinal roots, by which they reach the sympathetic.

The vaso-motor centre exerts a tonic or continuing action on the vessels, holding them in a state of partial constriction or *tone*. In this it may possibly be said to have an automatic action. Though tonic state of activity of the centre may be called automatic, it is really under the control of many complex reflex influences, which constantly vary the general tone, or effect local changes in the degree of constriction of this or that vascular area. Among the most striking afferent regulating impulses are those arriving from the heart, the digestive organs and the skin. In some animals, a special nerve—the depressor—has been discovered, which, passing from the heart to the medulla, keeps the vaso-motor centre informed as to the degree of tension, &c., of the heart cavities. When the heart becomes over-full, impulses pass from it and check the tonic power of the centre so as to reduce the arterial pressure against which the ventricle has to act. Electric stimulation of this nerve causes a remarkable fall in the general blood pressure. The vaso-motor centres regulate the distribution of blood to the viscera and skin, according to the condition of activity of these parts as described in another chapter (XXXI.).

The Cardiac Centre.

Although the heart beats with characteristic periodicity when cut off from the nervous centres, its normal rhythm is under the control of a group of nerve cells in the medulla, from which some of the fibres of the vagus conduct special regulating impulses. The action of this centre is habitually that of a restraining agent lessening the rate of the heart's contractions, and is hence called a tonic inhibitory centre (see page 222). The activity of the centre is influenced by the condition of many distant parts, such as the cortex of the brain, the abdominal viscera, &c., which exert a kind of reflex action on the heart through this centre. The degree of inhibitory power, as well as the share taken in the action of the centre by automatism and reflection, differs in different animals.

In the medulla there also exist many other centres connected with the organic functions. Among these the centres for swallowing and vomiting may be mentioned. For further details on this subject, the reader may consult the chapter on Digestion (see page 83).

CHAPTER XXXVI.

THE BRAIN.

As we pass upwards in attempting to trace the destiny of the conducting channels of the medulla, we come to the more elaborate system of nervous textures which, together, are called the brain. This is anatomically the most highly developed, and physiologically the most intricate part of the central nervous organs. Besides the nerve cells and various kinds of conducting channels with which we have already become familiar in the cord, &c., there are in the brain a vast number of smaller elements which do not possess the distinctive characters of cells. These granular bodies are tightly packed together in many parts of the centres, and must have some important function, which is, however, at present unknown.

The best way to get an idea of the general plan of construction of the brain, is to follow its development in the earlier stages of the embryo, from the time when it forms an irregular and thickened part of the tube of tissue destined to become the spinal cord. From this it will be seen that the brain is but a modified part of the primitive nervous axis, in which certain swellings may be observed at an early period of embryonic life. These swellings are called the fore-brain, the mid-brain, and the hind-brain, and in the future development of the parts give rise to (1) the hemispheres and basal ganglia; (2) the corpora quadrigemina, pons, and cerebellum; and (3) the medulla oblongata. The great mass of the brain—the hemispheres—are formed by an excessive development of bud-like processes which grow out from the sides of the fore-brain at an early period, which become elaborately folded, so that in the adult it is difficult to trace the relationship to the original form (compare p. 571, &c.).

The cells of the brain are, like those in the cord, grouped together in the complex grey substance, while the white part is made up exclusively of conducting fibres. The grey substance may be said to be distributed in four more or less distinct regions. (1.) Of these one can be traced along the floor of the fourth ventricle, from the matter of the cord to the base of the brain, as far forwards as the tuber cinereum, so that it may be said to be representative of the grey matter forming the inner lining of the primitive nervous tube. (2) Then come the ganglia of the brain, which are the more or less isolated masses of grey substance within the brain, known as the corpora quadrigemina, optic thalami, corpora striata, &c. (3) The grey substance of the cerebellum and of the corpora quadrigemina is derived from the upper part of the mid-brain. (4) The cortex of the hemispheres of the brain forms the most extensive grey district, and must be regarded as quite distinct from the preceding.

Connecting the various parts of these grey regions are sets of fibres, which may be classified as follows :—

1. Those which act as channels of intercommunication between the different parts of the same region. These may be divided into *unilateral*, which connect together the cells of a single hemisphere, and *bilateral*, or commissural fibres, which unite the corresponding masses of grey matter on the two sides of the brain.

2. Those which connect the different regions one with another. Under this head naturally fall (1) those fibres which pass between the cortex and the basal ganglia ; (2) those running from the cortex to the cerebellum ; and (3) those connecting the above with the axial or spinal grey matter.

THE MESENCEPHALON AND CEREBELLUM.

In examining the functions of the brain, it will be advantageous to consider the various parts in the order they are found in proceeding from the medulla towards the cerebral hemispheres. Between the medulla oblongata and the hemispheres, we thus come to a group of parts, including the pons, the corpora quadrigemina, pons varolii, and cerebellum, which may be called the mesencephalon, being developed from the mid-brain. The duties of this part of the nervous centres can be investigated by observing the actions of lower animals, in which the hemispheres have been removed, or the parts directly stimulated, and by noting the symptoms produced in man by lesions of this part of the brain. The former gives the most definite results, and therefore, for our purpose, deserves most attention.

When the cerebral hemispheres have been removed from a frog, the animal retains the power of carrying out co-ordinated motions of much greater complexity than those performed by command of the spinal cord alone. But this power is not exercised spontaneously. *That is to say, the* animal can balance itself accurately, jump, swim, swallow, &c., but it only attempts these acts when forced to do so by stimulations arising from its outer surroundings. Thus on a flat surface it sits upright, but does not stir from the spot where it has been placed; if the surface upon which it sits be inclined, so that its head is too low, it turns round to regain its equilibrium. If the surface be further inclined, it at first crouches so as not to slip off, and then crawls upwards to find an even resting place. Plunged into deep water, it swims perfectly, but on arriving in a shallow part it either rests quietly with its nose out of the water and its toes touching the ground, or crawls out to sit on the water's edge, where it finds its balance. When touched on the leg, it jumps away from the stimulus, and in so doing avoids any obvious dark obstacle. It swallows if a substance be put in its mouth, but it does not attempt to eat even when surrounded with food. In short, all movements, even the most complex, may be brought about by adequate stimulation—*spontaneity* only is wanting. The pupil responds by reflex contraction, when the retina is exposed to light; the eyes are closed if the light be intense; and the head may follow the motions of a flame moved from side to side. A sudden or loud noise causes the animal to move. From the foregoing facts, and the power such a frog has of avoiding a dark object, we may conclude that the impulses arriving from the special sense organs are all duly received and excite more or less elaborate response, but the *consciousness* of the arrival of these impulses no longer exists.

The removal of the hemispheres of birds and rabbits leaves the animal in somewhat the same condition; but the response to the special sense impulses is not so definite or well marked since the animal flies or runs against even the most obvious obstacles.

We may conclude, then, that while the medulla controls the co-ordinated movements absolutely necessary for the vegetative functions, the mid-brain (including the cerebellum of birds and mammals) controls the still more complex associations of co-ordinated movements necessary for the perfect performance of such acts as balancing our bodies, and enables us at the same time to carry on elaborate co-ordinated motions with the upper extremities, or vocal and respiratory muscles.

The enormous number of muscles simultaneously used in some of our commonest daily actions, concerning which we have but little thought, and take no voluntary trouble, shows the great importance of this part of the brain. If we take a simple example, that of standing in the upright position (*equilibration*) (see page 339) we find that a great number of muscles have to act together with the most exact nicety to accomplish what, even in man, is a quite thoughtless, if not quite involuntary, action. In the frog, as has been seen, equilibration is performed by reflex action alone. In man, the nervous mechanisms are probably more complicated by his erect attitude and the addition of the cerebellum, &c., but they are nevertheless comparable with those of the frog. It may therefore be instructive to examine the details of the mechanisms in a frog deprived of its cerebral hemispheres.

The optic lobes (which correspond to the corpora quadrigemina, and also take the place of the cerebellum of the higher animals) form, in the frog, the great centres of equilibration, locomotion, &c. If these lobes be destroyed, the animal can no longer sit upright, jump, or swim. The first point to determine is, whence do the impulses arrive which bring about these complex co-ordinations. The first set are those coming from the tactile sense of the skin of the parts touching the surface; another set of impulses arrives from the acting muscles acquainting the centres with the amount of work done. A third set comes from the eyes, by which the position of the surrounding objects is gauged; and finally, from the semicircular canals of the internal ear come impulses which inform the equilibrating centres as to the position of the head.

By depriving a frog of these several portals by which incoming stimuli direct the balancing centres, it can be rendered incapable of any of the acts requiring equilibration, even when the regulating centres are intact. In our own bodies we can convince ourselves of the absolute importance of these afferent regulating impulses arriving from the ear, eye, skin, and muscles. If having bent one's forehead to the handle of a walking stick, the end of which is fixed on the ground, we run three or four times around this axis, and then quickly walk towards any near object, we find how helpless our volition becomes if deprived of the normal incoming stimulus, for thus an unwonted disturbance of the nerve-terminals in the semicircular canals has dispatched conflicting impulses to the co-ordinating centre of equilibration. Further, we know that we stand less fixedly when our eyes are shut, and we move unsteadily when our feet are benumbed, &c.

Crura Cerebri.

Passing above the *Pons Varolii*, we come to a thin isthmus, composed of two thick strands of nerve substance connecting the mesencephalon with the cerebral hemispheres. These are called the crura cerebri. They diverge slightly in their upward course towards the hemispheres, and lie just below the corpora quadrigemina, which have already been referred to. Minute examination of these crura brings to light an anatomical difference which corresponds with a distinct physiological separation between the paths taken by the sensory and motor impulses in each crus. The lower or more anterior part, which can be seen on the base of the brain, is called the base or *crusta*. This is made up of motor nerve channels only. The posterior or upper part, which lies next to, and is connected with the corpora quadrigemina, is called the *tegmentum*, and is composed of sensory fibres. Anatomically the separation between the two is indicated by some scattered nerve-cells (*locus niger*). The base, or crusta, which is the great bond of union between the spinal cord and the cerebral motor centres, passes into the corpus striatum; and the tegmentum, or great sensory tract, is directly connected with the optic thalamus.

BASAL GANGLIA.

The great masses of grey and white matter seen on the floor of the lateral ventricles are called the *corpora striata* and *optic thalami*, and together are spoken of as the basal ganglia. The exact relationship borne by their functions to those of the mesencephalon and cerebral cortex is not perfectly understood, though it is, no doubt, intimate. The following are some of the more important points in the evidence on the subject:—

CORPORA STRIATA.—The motor tracts, coming from below, lie in the lower part of the crus cerebri, and thence one on each side passes into the corresponding corpus striatum. Anatomically, then, this part may be regarded as the ganglion of the motor tract.

Destructive lesion of one corpus striatum is followed by loss of power of the muscles of the other side of the body. This is equally true of lesions artificially produced in animals, and those resulting from disease in man. When the crura on both sides are destroyed the animal remains motionless and prostrate.

Electrical stimulation of one of the corpora striata causes unilateral motions of the other side of the body. This fact, however, does not teach us much concerning the functions of the particular cells of its grey matter, since the stimulus cannot be kept from affecting the fibres passing through the corpus striatum to go directly to the motor tract.

In dogs, and still more so in rabbits, the corpora striata seem to be able to carry out some complex motions which in man are believed to require the co-operation of the higher cerebral centres. It has been stated that a dog whose cerebral cortex is completely destroyed can perform movements that in man can only be evoked by the cortex *of the hemispheres*.

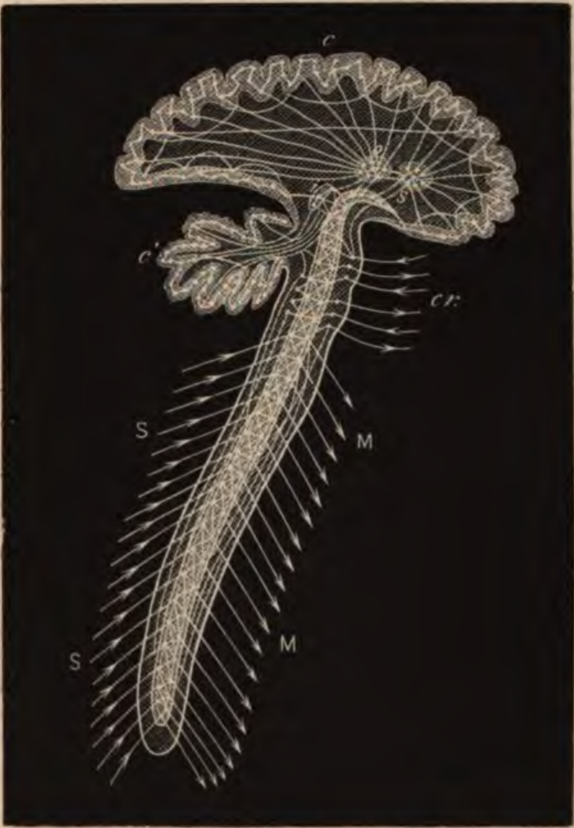


Fig. 244.—Diagram of some of the paths taken by nerve impulses in the brain and spinal cord.
C. Grey substance of cerebral cortex. *c'.* Grey substance of cerebellum.
Cr. Cranial nerves, some afferent and some efferent.
M. Motor (efferent) spinal nerves. *S.* Sensory (afferent) spinal nerves.

cerebri. They diverge slightly in their upward course towards t hemispheres, and lie just below the corpora quadrigemina, whi have already been referred to. Minute examination of these cr brings to light an anatomical difference which corresponds with distinct physiological separation between the paths taken by t sensory and motor impulses in each crus. The lower or more anter part, which can be seen on the base of the brain, is called the bas *crusta*. This is made up of motor nerve channels only. The po terior or upper part, which lies next to, and is connected with t corpora quadrigemina, is called the *tegmentum*, and is composed sensory fibres. Anatomically the separation between the two indicated by some scattered nerve-cells (*locus niger*). The base, crusta, which is the great bond of union between the spinal cord a the cerebral motor centres, passes into the corpus striatum; and t tegmentum, or great sensory tract, is directly connected with the opt thalamus.

BASAL GANGLIA.

The great masses of grey and white matter seen on the floor of t lateral ventricles are called the *corpora striata* and *optic thalami*, w together are spoken of as the basal ganglia. The exact relationsh borne by their functions to those of the mesencephalon and cerebr cortex is not perfectly understood, though it is, no doubt, intimat The following are some of the more important points in the eviden on the subject:—

CORPORA STRIATA.—The motor tracts, coming from below, lie the lower part of the crus cerebri, and thence one on each si passes into the corresponding corpus striatum. Anatomically, th this part may be regarded as the ganglion of the motor tract.

Destructive lesion of one corpus striatum is followed by los power of the muscles of the other side of the body. This is equal true of lesions artificially produced in animals, and those resulti from disease in man. When the crura on both sides are destroy the animal remains motionless and prostrate.

Electrical stimulation of one of the corpora striata causes u lateral motions of the other side of the body. This fact, howev does not teach us much concerning the functions of the particul cells of its grey matter, since the stimulus cannot be kept fro affecting the fibres passing through the corpus striatum to go direct to the motor tract.

In dogs, and still more so in rabbits, the corpora striata seem to able to carry out some complex motions which in man are believed to require the co-operation of the higher cerebral centres. It has

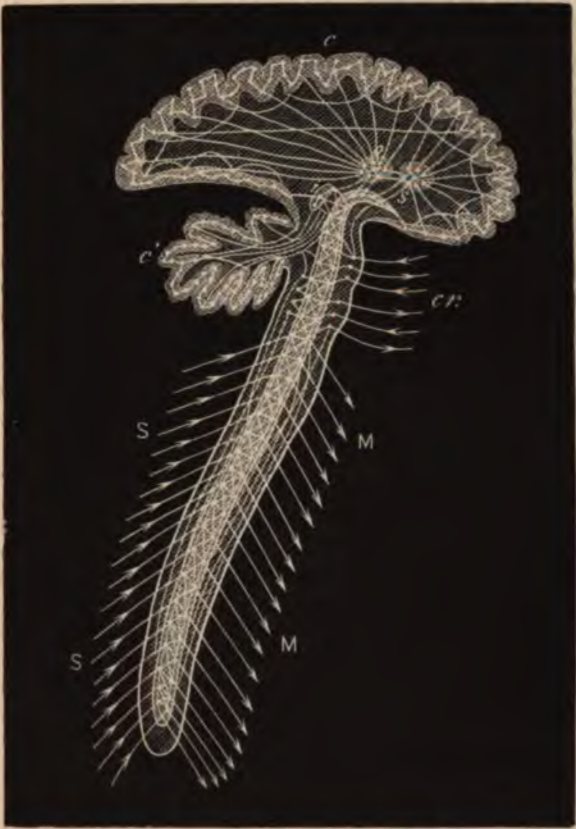


Fig. 244.—Diagram of some of the paths taken by nerve impulses in the brain and spinal cord.

C. Grey substance of cerebral cortex. *c'.* Grey substance of cerebellum.
Cr. Cranial nerves, some afferent and some efferent.
M. Motor (efferent) spinal nerves. *S.* Sensory (afferent) spinal nerves.

been stated that a dog whose cerebral cortex is completely destroyed can perform movements that in man can only be evoked by the cortex of the hemispheres.

It would appear then that the grey matter of the corpus striat is a motor ganglion, nearly related in function to the cerebral cort The cells of this ganglion are the first agents working under t direction of the cortical centres, and carry out the organisati and distribution of voluntary motor i pulses. In animals whose hemispher are less complexly developed, such the dog or rabbit, the "basal agen seems capable of carrying on more ela rate work, independent of the guidan of the higher motor centres in the gr matter of the brain.

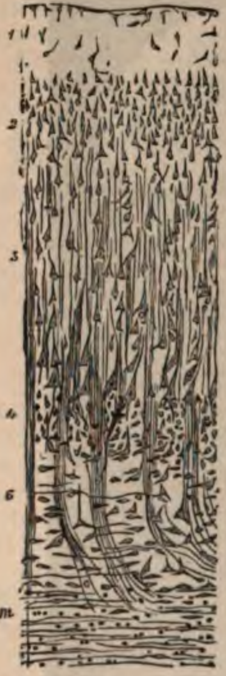


Fig. 245.—Section through the grey matter of the brain of man, showing several layers of cells into which fine fibres pass from below.

OPTIC THALAMI.—The evidence co cerning these ganglia is far from being satisfactory or conclusive as that relati to the corpus striatum.

Anatomically the matter is equally clea they are the ganglia of the sensory tra since the tegmentum or sensory parts the crura pass directly into them. The form, in fact, the only routes by which impulses giving rise to the different kin of sensory impressions can arrive at th cerebral cortex. But the evidence we c obtain by the physiological examination sensory impressions is very indistinct comparison with the obvious results w find when motor tracts are excited; indee in the complete absence of all mot it is difficult to know whether an anim feels or not, as we have no signs to sh whether the stimulus takes effect. Fu ther; it is difficult, as has been alre seen, to stimulate any sensory tract wi out the impulse being reflected to motor neighbours, so a muscular mo ment often results from stimulation of a group of cells purely sens in function.

When we take into consideration the foregoing points, and fact that it is difficult, if not impossible, to destroy a portion of bra substance without irritating it and the neighbouring structures, cannot be surprised that experimenters have arrived at very tradictory results, both by stimulating and destroying the optic thalami. Some find that electric stimulation causes muscular movements; others find that it does not. Some authorities state that destruction of the optic thalami interrupts only the incoming sensory impressions; others say it gives rise to motor paralysis.

Human pathology helps us but little, for it is impossible to say whether a given lesion simply abolishes the function of the part or acts as an irritant to it, or in some degree produces both these effects. Local lesions of the optic thalami have been met with, in some of which sensory, and in others, both sensory and motor defects have been observed in the patients.

We must, then, remember that the occurrence of motion as the result of stimulation, or the absence of muscular power as the result of destruction of the optic thalami must not be accepted as conclusive evidence of the motor function of the active elements—the nerve-cells—of this part, because these results may depend on the indirect influence of the sensory impulses coming from these cells.

CEREBRAL HEMISPHERES.

It is now universally regarded as a recognised fact that in man the hemispheres of the brain are the seat of the mental faculties—perception, memory, thought, and volition. The cerebral cortex is the part of the nervous system in which the subjective perception of the various sensory impulses takes place, and in which impulses are converted into impressions or mental operations. It is in the cortical nerve-cells the so-called voluntary impulses, causing movement of the skeletal muscles, have their origin. It is thus a sensory and a motor organ. But it has a far wider range of function than is expressed by saying it is both sensory and motor; indeed, in this it would be no better than the other nerve-centres in the spinal cord, &c. The cells of the cortex of the brain seem to differ from those of the lower nerve-centres (which can also receive, and at once send out, corresponding impulses), in this: when an impulse arrives at the cerebral cells, it there excites a change, which, besides producing an immediate effect, leaves a more or less permanent impression; the impression persists, and if the cell be well supplied with chemical energy in the shape of nutriment, the impression may be reproduced at a subsequent period. This revival of impressions, the effects of past stimulations, or "re-collection" is exclusively the property of the cerebral cortex, and to it the hemispheres owe their mental faculties. During our lifetime sensory impulses are continually

The leading experimental experiences which have been recorded are the following:—

1. Extensive tracts of the cortex of the hemispheres may be removed, by accident or experiment, without interfering with the cerebral functions in any marked or tangible way. Both men and animals have lived for years, after the loss of a considerable quantity of brain substance, without showing impairment of either mental or bodily faculties.

2. Lesion of a certain part of the frontal lobe of the left hemisphere of man (posterior part of the third frontal convolution) has been so frequently followed by the loss of the faculty of speech—aphasia—that pathologists now call that spot the centre of speech.

3. Destruction of the convolutions around and in the neighbourhood of the fissure of Rolando gives rise to temporary loss of power in the limbs of the other side, voluntary motion being abolished when an extensive area is destroyed. This loss of power is more obvious in animals with complex brains (man and monkey) than in those less highly organised (dog, cat, rabbit), which rapidly recover.

4. Destruction of the surface of the posterior lobes interferes with the reception of visual impressions, and if an area, including the angular gyri and all the posterior lobes be destroyed, the animal remains blind.

5. Extensive areas of the brain surface may be stimulated mechanically, chemically, or electrically, without the least response being shown by the animal, to indicate either sensory or motor excitations.

6. Stimulation of the convolutions around the fissure of Rolando, however, gives rise to definite co-ordinated movements of muscles of the other side of the body. Indeed, local groups of muscles respond with surprising constancy to the electric stimulation of certain definite parts of the cortex. These convolutions have thus been mapped out into motor centres for hind limb, fore limb, face, &c.

From this we are tempted to conclude (1) that the cortex of the posterior region of the hemispheres is related to the reception of some sensory impressions; (2) that the superior and lateral part in the neighbourhood of the fissure of Rolando is related to the discharge of voluntary motor impulses; and (3) that the anterior lobes are not immediately subservient to either the sensory or motor functions of the hemispheres, though the centre presiding over the faculty of speech is placed in this part on the left side.

As an objection to the soundness of these conclusions, the remarkable and undoubted fact has been urged, that no matter how thorough is the destruction of the centres, the function returns after the lapse of a variable interval. In some instances the loss of function only remains for a few hours after the operation; in other cases (those in which the injury is extensive and deep, and the animal belongs to a class with high mental organization) the recovery is slow and may extend over several weeks and months. In man and monkeys the function may be lost for ever, and the nerve channels, which formerly carried the impulses to or from the injured centre, become degenerated.

From some of the foregoing facts—viz., the constant and regular response of certain groups of muscles to the stimulation of certain local spots of the brain surface, and the temporary destruction of the functions of some organ when a certain point is injured—it seems definitely fixed that certain local parts of the brain surface are in more immediate connection with certain peripheral organs than are others, and that these local areas have been in the habit of receiving (in the case of the visual impulses coming to the angular gyri) or sending out (in the case of motor impulses starting from the motor centres) impulses of a special and definite kind.

From the other facts mentioned—viz., the recovery of function after injury, or the complete absence of functional lesion—we must conclude that these local areas are by no means the only agents which can carry on the business of receiving for the mind impulses from the periphery, and sending out voluntary impulses to the muscles; but that rather there are many groups of nerve-cells, in relation with the nearest sub-agents—the basal ganglia—which can take on the duty of the injured cells, and act as cortical centres, receiving sensory, and discharging motor impulses. In respect of this capability of one part of the cerebral cortex to carry on the duties ordinarily allocated to another, we have a complete analogy in the grey part of the spinal cord. Partial section of the grey part of the spinal cord (even if it be cut at two or three different levels) does not destroy the sensation of any local area of skin, showing that the delicate felt-work of nerve fibrils in the grey substance can conduct the impulses in many directions, so that even when a considerable number of the ordinary routes are blocked by section of fibrils and destruction of the cells at the part cut, the neighbouring channels can carry on the work, so that after a little time the sensory impulses are carried from all parts ot the skin to the brain without delay.

It has already been pointed out that the function of any given nerve fibre depends on the function of its terminals. The fibre itself is merely a conducting agent. In somewhat the same way the functions of any given nerve-cell must depend on the number and character of its connections. If it be attached to a motorial end-plate in a muscle, it can only be an exciter of impulses that give rise to motion : if it be connected only with a sensory terminal, it can only be a receiver of sensory impulses. But, in the grey matter of the spinal cord, and still more so in that of the cerebral cortex, we may assume that all the cells are in more or less intimate connection with innumerable other cells. In fact, we must imagine that the whole of the grey matter of both cord and brain is interwoven into a complex felt-work of fibrils and cells, which in no part are isolated from the rest, but that all the elements form a continuous system.

CHAPTER XXXVII.

REPRODUCTION.

ORIGIN OF MALE AND FEMALE GENERATIVE ELEMENTS.

ONE of the chief characteristics of a living being is the power it possesses of reproducing itself; that is to say, organisms can, under favourable conditions, form out of themselves other living bodies with similar lives and habits.

In the lowest forms of animal life this propagation of species may take place by the division of a single cell; thus an amœba reproduces its like by the cleavage of its mass of protoplasm, which separates the main body into two amœbæ. In such a case the method of reproduction is purely *asexual*, the amœba containing within itself the power of forming other amœbæ without help from other individuals.

As we ascend the animal scale, we find that just as other functions are allotted to certain groups of cells, specially differentiated for the purpose, so the function of reproduction is performed by certain specially modified collections of cells. Further, we find the fact that the production of a new being requires the co-operation of two kinds of generative elements, each of which is commonly produced by a different reproductive organ. These reproductive organs in the higher animals are placed in different individuals of the same species. This divides most organisms into male and female sexes, and is hence termed the *sexual* method of reproduction.

The sexual method of reproduction is met with in all the more highly developed forms of animal and vegetable life. The male organ produces active elements—the *spermatozoa*; the female organ produces the *ovum*, which, when fertilised by the spermatozoon, develops into the embryo.

In mammalia the uterus is the most important of the subsidiary organs, as it is modified for the development and growth of the embryo: its function, however, can be performed by other organs, as is seen in cases of extra-uterine fœtation, when the ovum is velops in some unusual situation, such as in the Fallopian tube, or in the abdominal cavity.

The spermatozoa are formed by the cells lining the tubuli seminiferi of the testicle. These cells are cubical masses of protoplasm, which undergo rapid proliferation. The nuclei divide, and from each part resulting from this division arises the head of a spermatozoon, and the body is developed from the protoplasm of the cell. The spermatic elements escape into the tubes, and pass down the vasa deferentia into the vesiculæ seminales, where they either undergo a retrograde change or are cast out of the body.

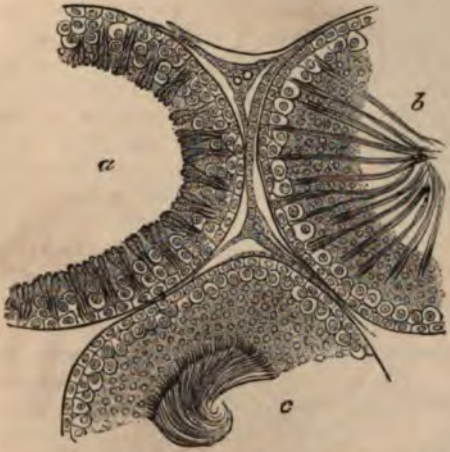


Fig. 246.—Section of the tubuli seminiferi of a rat. (Schäfer.)
a, Tubuli in which the spermatozoa are not fully developed.
b, Spermatozoa more developed. *c*, Spermatozoa fully developed.

The ovum arises from the differentiation of one of the cells of the *germ-epithelium* covering the surface of the ovary. A group of these cells entering the periphery of the ovary, becomes there embedded in a kind of capsule derived from the surrounding areolar tissue of the stroma, and forms an immature *Graafian follicle.* One of the cells grows rapidly to become the ovum, the rest increase in number to form the small cells of the granular tunic. As the follicle develops, it works its way towards the centre of the ovary, and then approaches the periphery of the organ as a fully-developed Graafian *follicle.*

Microscopically, it is seen to be surrounded externally by a capsule—the *tunica fibrosa*, which is ill-defined from the stroma of the ovary in which it lies. Beneath this is a layer of capillary blood-vessels, the *tunica vasculosa*, and to these two coats collectively the term *tunica propria* is applied.

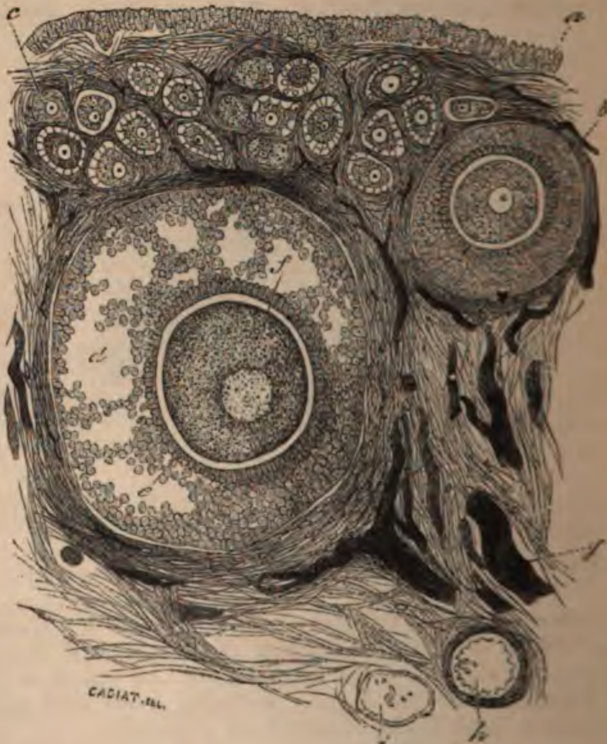


Fig. 247.—Section of the ovary of a cat, showing the origin and the development of Graafian follicles. (Cadiat.)

a. Germ-Epithelium.
b. Graafian follicle partly developed.
c. Earliest form of Graafian follicle.
d. Well developed Graafian follicle.
e. Ovum.
f. Vitelline membrane.
g. Veins.
h, i. Small vessels cut across.

Inside the tunica propria are granular cells of small size, which occupy a considerable space in the follicle; they are heaped up at one spot to receive the ovum, which lies embedded in their midst. These cells receive the name of the *tunica granulosa*, and their projecting portion, which encircles the ovum, is called the *discus proligerus*. Filling up the remainder of the follicle is a fluid—the *liquor folliculi*. The surface of the ovary is covered by columnar cells, which are continuous with the endothelial cells of the peritoneum. When the follicle is fully matured, it lies at the periphery of the ovary beneath this layer of cells, which separates it from the abdominal cavity.

MENSTRUATION AND OVULATION.

After puberty, at intervals averaging about four weeks, the genital organs of the female become congested, and at the same time a Graafian follicle is ruptured and its contained ovum set free. Coincidently with the rupture of the follicle, the fimbriated extremity of the Fallopian tube becomes closely approximated to the spot where the follicle lies, so that the ovum instead of falling into the abdominal cavity, passes into the canal of the Fallopian tube, down which it is conveyed to the uterus.

The usual place for the ovum to meet the spermatozoa, and to be impregnated, is the Fallopian tube.

When the ovum reaches the uterus, if it be unimpregnated, it is cast out with the surface cells of the mucous membrane of the uterus, which are destroyed, and escape along with a sanious fluid. The whole of these phenomena constitute a menstrual act.

If, however, the ovum become impregnated, it remains in the Fallopian tubes some days, during which time the mucous membrane of the uterus becomes so hypertrophied and developed as to retain the ovum when it reaches that organ.

The human ovum is a cell consisting of a mass of protoplasm enclosing a nucleus and a nucleolus, and surrounded by a cell-wall. On its outer surface is an irregular layer of cells, the remains of that part of the tunica granulosa which encircled the ovum in the Graafian follicle. The cell-wall of the ovum is called the *vitelline membrane* or *zona pellucida*, and the mass of granular protoplasm it encircles, the *vitellus* or yolk, and in this is a nucleus—the *germinal vesicle*, which contains a nucleolus—the *germinal spot*.

Beneath the outer covering of calcareous material of the hen's egg there is a white membrane, which encloses a transparent albuminous substance known as the white of egg. Inside this is a yellow fluid mass, the yolk, which is surrounded by a delicate membrane, the *vitelline membrane.* The yolk is made up of two varieties of material of different shades of colour, the white and the yellow yolk. Of these the yellow forms the greater part, the white being arranged in thin layers, which separate the yellow yolk into strata. In the centre of the yolk it forms a flask-shaped mass, with its neck turned to the upper surface, upon which a portion of the yolk called the *cicatricula* rests. This cicatricula, which lies between the vitelline membrane and the white yolk, is the active growing part of the egg, and out of it is developed the chick and the embryonic membranes.

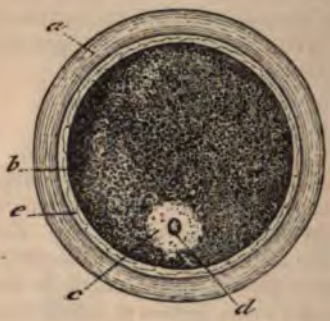


Fig. 248.—Ovum. (Robin.)

a. Zona pellucida or vitelline membrane.
b. Yolk.
c. Germinal vesicle or nucleus.
d. Germinal spot or nucleolus.
e. Interval left by the retraction of the vitellus from the zona pellucida.

Extending through the albumin from the vitelline membrane to the ends of the egg are two twisted membranous cords—the chalazæ, which fix and protect the delicate yolk from shocks, but allow it to rotate, so that the cicatricula is always the uppermost part of the yolk when the egg is on its side.

The main structural differences between the human ovum and that of a fowl are apparent from the above description : the essential peculiarity of the development of the hen's egg is that only a portion of the yolk is engaged in the formation of the first signs of the chick and its membranes, by far the greater part of the egg both yolk and albumin being utilised in supplying the nourishment during the subsequent stages of development.

After the egg has been laid, it obtains no help from the outside world, except the oxygen of the air and the heat of the mother's body ; it is, as it were, fenced in with a protecting membrane, garrisoned with the quantity of provisions required, and by the warmth of the hen's body stimulated to growth and activity.

The whole of the human ovum, on the other hand, undergoes segmentation and differentiation in the primary formation of the embryo, which subsequently is supplied with the necessary nourishment from the maternal circulation. The life and growth of the human embryo, in fact, depends entirely upon supplies from the mother, the ovum not having within itself any store of nutrient material.

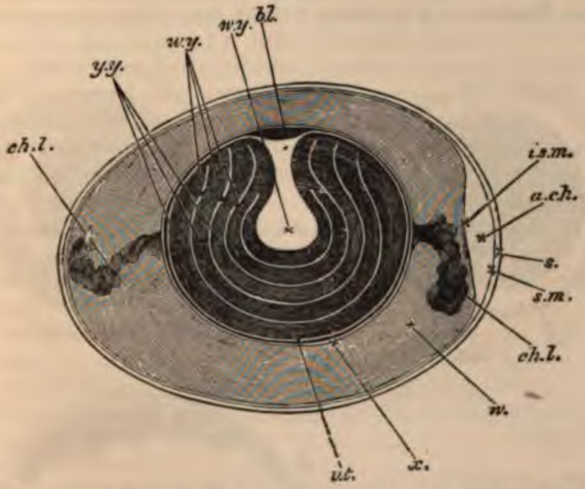


Fig. 249.—Diagram of a section of an unimpregnated fowl's egg. (From Foster and Balfour, after Allen Thomson.)

bl. Blastoderm or cicatricula.
w.y. White yolk.
y.y. Yellow yolk.
ch.l. Chalaza.
i.s.m. Inner layer of shell membrane.
s.m. Outer layer of shell membrane.
s. Shell.
a.ch. Air space.
w. The white of the egg.
vt. Vitelline membrane.
x. The denser albuminous layer which lies next to the vitelline membrane.

CHANGES IN THE OVUM SUBSEQUENT TO IMPREGNATION.

The first changes in the ovum independent of impregnation consist in the shrinking of the yolk from the vitelline membrane, and the extrusion from it of certain granular bodies which lie between it and the vitelline membrane, and are called the *polar globules.* The germinal spot and germinal vesicle also disappear, and are thought, by some observers, to form these polar globules. After the union of the male and female elements, a new nucleus *appears in the* vitellus which forms what is called the segmentation sphere. This divides at first into two segments, then into four, eight, sixteen, and so on, until a large mass of cells occupies the yolk. To this condition the name of *morula* is given, from its supposed likeness to a mulberry. Fluid now collects among the cells and separates some of them from the others, and the cells arrange themselves into an outer layer and an inner layer, consisting of different kinds of cells. The inner cells finally become aggregated at one part of the ovum in contact with the outer cells. The ovum now receives the name of the *blastodermic vesicle.*

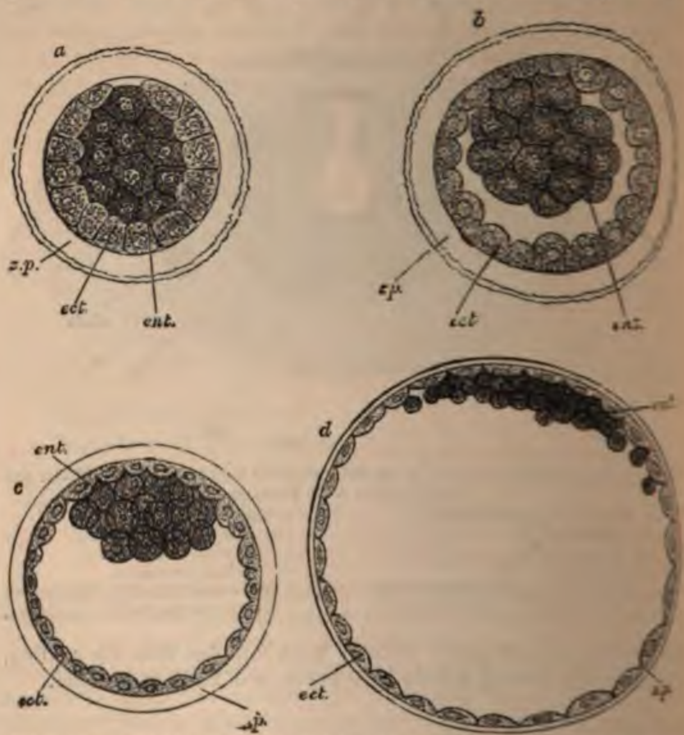


Fig. 250.—Sections of the ovum of a rabbit showing the formation of the blastodermic vesicle. (E. Van Beneden.)

a, b, c, d, are ova in successive stages of development. *zp*, Zona pellucida. *ect*, Ectomeres, or outer cells. *ent*. Entomeres, or inner cells.

In the hen's egg the cleavage is confined to the cicatricula or blastoderm, and does not include the rest of the yolk. Such an ovum, from the fact that the cleavage of the yolk is only partial, receives the name of *meroblastic*. The human ovum, which undergoes complete segmentation, is called a *holoblastic* ovum.

The cells in the blastodermic vesicle become arranged into three definite layers, which are called respectively, from their position in the blastoderm, the *epiblast*, the *mesoblast*, and the *hypoblast*.

From these layers are developed the embryo and the membranes surrounding it, each layer being developed into certain tissues and forming these only.

Thus from the epiblast, or outer layer, arise the epidermis of the skin, the brain and spinal cord, and certain parts of the organs of special sense; whilst it also aids in the formation of the chorion and the amnion. From the mesoblast are developed the skeleton, the connective tissues, the muscles, the nerves, in addition to the vascular system and the supporting tissue of the glands; one kind of tesselated cells arise from this layer, viz., the endothelium, forming the surface of all serous membranes. From the hypoblast springs the epithelial lining of the alimentary canal, of the glands which are diverticula from it, and of the lungs; it also forms the lining membrane of the allantois and yolk sac.

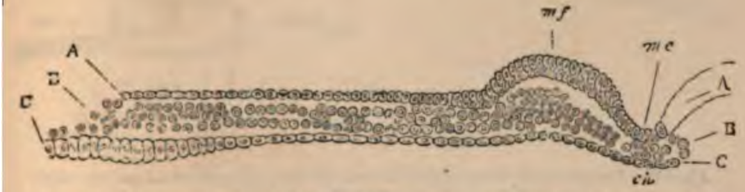


Fig. 251.—Transverse section of the medullary groove, and half the blastoderm of a chick of eighteen hours. (Foster and Balfour.)

A. Epiblast.
B. Mesoblast.
C. Hypoblast.
mf. Medullary fold.
mc. Medullary groove.
ch. Notochord.

The blastoderm of the hen's ovum, which is comparatively easily studied, consists of a small clear central portion, called the *area pellucida*, from which the body of the chick arises. Surrounding the area pellucida is a much larger zone, which appears less transparent; this, the *area opaca*, is devoted to the formation of the membranes.

The embryo is developed from the rest of the blastoderm in the following manner. At the front of the area pellucida a fold, or dipping in of the blastoderm takes place; this consists of a projecting part or fold above and a groove below, and constitutes what is known as the *cephalic* or head fold. The upper projecting portion of the fold tends to grow forwards, whilst the groove grows gradually backwards. Later on, another fold appears at the posterior part of the area pellucida, this is the tail fold. At the sides of the area pellucida folds appear, which tend to grow downwards and inwards so as to reach the under surface of the blastoderm and unite with the head and tail folds.

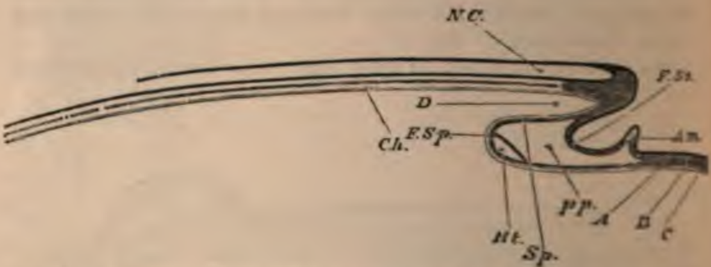


Fig. 252.—Diagrammatic longitudinal section through the axis of an embryo chick (Foster and Balfour.)

N.C. Neural canal.
Ch. Notochord.
D. Foregut.
F.So. Somatopleure.
F.Sp. Splanchnopleure.
Sp. Splanchnopleure forming the lower wall of the foregut.
Ht. Heart.
pp. Pleuroperitoneal cavity.
Am. Amniotic fold.
A. Epiblast.
B. Mesoblast.
C. Hypoblast.

By the approximation of all these folds a canal is formed—the *embryonal sac*—which is closed above by the main portion of the area pellucida, in front by the head fold, behind by the tail fold, at the sides by the lateral folds, whilst below it is open to the vitellus. This canal ultimately becomes subdivided into an inner tube, the alimentary tract, and an outer one, which forms the body walls, the final place of union of the folds being marked by the umbilicus. It must be clearly understood that these primary folds which form the embryo include in their layers the epiblast, the whole thickness of the mesoblast, and the hypoblast, whereas the folds giving rise to the membranes do not comprehend all these layers.

FORMATION OF THE MEMBRANES.

(1) *The Amnion.*—The mesoblast around the embryo becomes thickened, and is split into two distinct layers; this cleavage is at first confined to the neighbourhood of the embryo, but gradually spreads over the whole blastoderm.

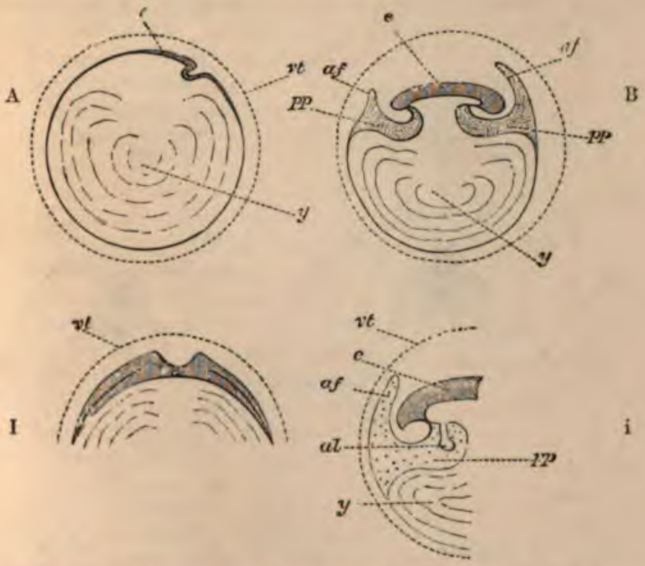


Fig. 253 and the following two woodcuts are diagrammatic views of sections, through the developing ovum, showing the formation of the membranes of the *bird's chick.* (Foster and Balfour.)

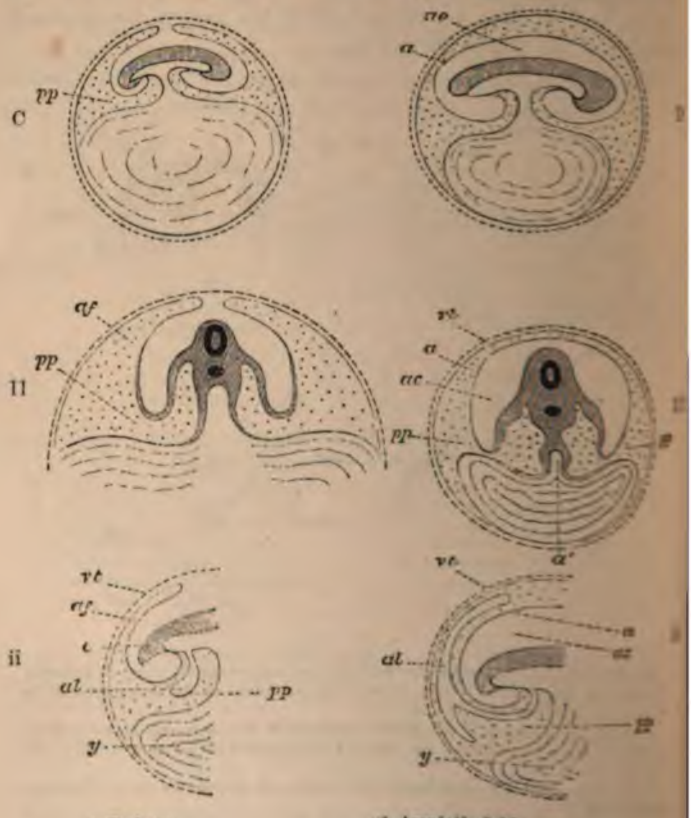
A, B, C, D, E, and F are vertical sections in the long axis of the embryo at different periods, showing the stages of development of the amnion and of the yolk-sac.

I., II., III., and IV. are transverse sections at about the same stages of development.

i., ii., and iii. give only the posterior part of the longitudinal section, to show three stages in the formation of the allantois.

e. Embryo.
y. Yolk.
pp. Pleuroperitoneal fissure.
vt. Vitelline membrane.
af. Amniotic fold.
al. allantois.

The upper of these two layers of the blastoderm receives the name of the *somatopleure,* and is engaged in the formation of the *body walls of the embryo* and the amnion. The lower one is called the *splanchnopleure*, and forms the walls of the alimentary canal, the allantois, and the yolk-sac. The space intervening between these layers is called the pleuroperitoneal cavity. At a point in front of the cephalic fold, an upward projection of somatopleure takes place, conveying with it the overlying epiblast. Along the sides of the embryo and behind the caudal fold, projections of the somatopleural mesoblast and epiblast also occur. Thus folds are develop-



e. Embryo.
a. Amnion.
a'. Alimentary canal.
vt. Vitelline membrane.
af. Amniotic fold.
ac. Amniotic cavity.
y. Yolk.
al. Allantois.

consisting of somatopleural mesoblast and of epiblast, which tend to grow upwards and meet over the back of the embryo. These folds are the amniotic folds, and each of them presents two surfaces, one looking towards the embryo and the other towards the vitelline membrane. As they meet over the back of the embryo the folds become fused, the membranes looking towards the embryo joining to form the amnion proper, whilst those next the vitelline membrane unite to form the *false amnion*, which, separating from the amnion proper, retires towards the vitelline membrane, with which it unites to form the primitive chorion.

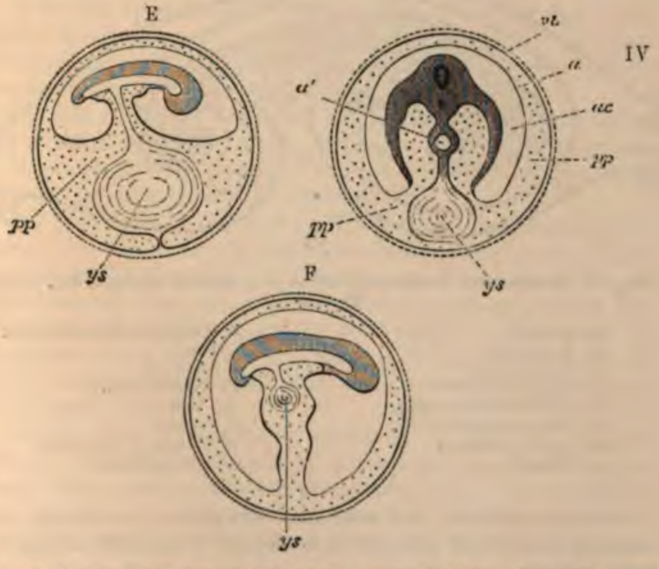


Fig. 254.—Diagrammatic sections of an embryo, showing the destiny of the yolk-sac, *ys*. *vt*, Vitelline membrane. *pp*, Pleuroperitoneal cavity. *ac*, Cavity of the amnion. *a*, Amnion. *a'*, Alimentary canal. *ys*. Yolk-sac.

The true amnion then is a sac formed of an outer layer derived from the mesoblast and an inner layer derived from the epiblast. The false amnion likewise consists of mesoblast and epiblast, but here the epiblast is external. The true amnion is continuous with the skin of the embryo, and when the fœtus is mature, the connection may be traced by the umbilical cord, around which it forms a sheath to be continuous with the skin at the umbilicus. The membranous sac enlarges, and in mammalia eventually becomes the large bag of liquid which contains the fœtus. The amniotic liquid is of low specific gravity, consisting mainly of water containing traces of nitrogenous matter, and also phosphates and chlorides.

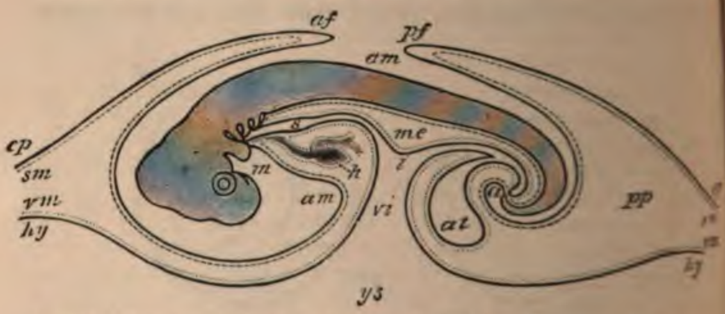


Fig. 255.—Diagrammatic longitudinal section of a chick on the fourth day. (Allen Thomson.)

ep,	Epiblast.	*a*,	Position of the future arm.
hy,	Hypoblast.	*h*,	Heart.
sm,	Somatopleure.	*i*,	Intestine.
v.m.	Splanchnopleure.	*vi*.	Vitelline duct,
af. pf,	Folds of the amnion.	*ys*,	Yolk.
pp,	Pleuroperitoneal cavity.	*s*,	Foregut.
am,	Cavity of amnion.	*m*,	Position of the mouth.
al,	Allantois.	*me*,	The mesentery.

It contains albumin and some other nitrogenous constituents, and a minute quantity of urea, which is thought to be derived from the fœtal kidneys.

This fluid preserves the child from the effects of any jolts or jars caused by the movements of the mother, and similarly protects the uterus of the mother by acting as a buffer between the fœtus and the uterine wall. Before delivery it helps to dilate the os uteri, so that when the amnion is ruptured the head of the fœtus occupies the opening which has been gradually made by the fluid wedge. The outer part of the amniotic membrane, derived from the mesoblast, is of a tougher character than the inner epithelial layer, and it is said to possess muscular fibre and to be capable of rhythmical contractions.

(2) *The Yolk Sac* is that part of the blastoderm which grows and envelops the yolk, which previously was only surrounded by the

vitelline membrane. After the mesoblast has split into two layers, the splanchnopleure becomes bent inwards at a point some distance from its origin, carrying with it the hypoblast. By this curve an upper constricted canal is differentiated from the large lower cavity. This upper canal becomes eventually the alimentary tract, the lower cavity the yolk-sac, whilst the constricted portion leading from the one to the other is the canal leading from the intestine to the yolk, called the *ductus vitello-intestinalis.*

At first the splanchnopleure encloses only the upper part of the yolk, but as development proceeds it grows around, and at last completely encircles it. The yolk-sac is thus derived from the splanchnopleural layer of the mesoblast, and its lining hypoblast.

The yolk is continually used up for the nutrition of the embryo, and its covering shrinks in size, becoming smaller with the growth of the fœtus, until eventually it forms but a shrivelled protrusion from the intestine, lying in the umbilical cord.

The importance of the yolk-sac differs largely in mammalia and birds. In man it is not highly developed, as its place is early supplied by the placenta. In birds, however, it develops to a much higher degree, being the seat of a special circulation, which carries nourishment from the yolk to the chick. The vessels are developed in the mesoblastic portion of the membrane, and are called the *omphalo-mesenteric vessels,* which convey blood to and from the primitive heart.

(3.) *The allantois,* or urinary vesicle, in the chick is of importance, as the vessels developed in it are used for respiratory purposes, being spread out beneath the porous shell. In the mammalian embryo it is still more important, as it is the seat of the circulation, which performs the chief function of the fœtal placenta. The allantois arises at the tail of the embryo, as a budding outwards of a portion of the splanchnopleure forming the wall of the primitive intestine. It is lined by hypoblast, and projects into the pleuro-peritoneal cavity. As it grows away from the embryo it extends between the layers of the true and false amnion and approaches towards the vitelline membrane, but remains connected to the intestine by a narrow tube. When it reaches the periphery of the ovum, it spreads over the chorion as a complete lining, and sends processes into the villi of that organ. It becomes chiefly developed, however, at that part of the chorion which is opposite the *decidua serotina* of the mother. In the mesoblastic layer of the allantois blood-vessels arise which are connected with large trunks, proceeding from the primitive aortæ, called the umbilical arteries; these will, however, be further described when treating of the fœtal placenta.

As the fœtus becomes developed, the part of the allantois in connection with the body becomes gradually obliterated. A part of it

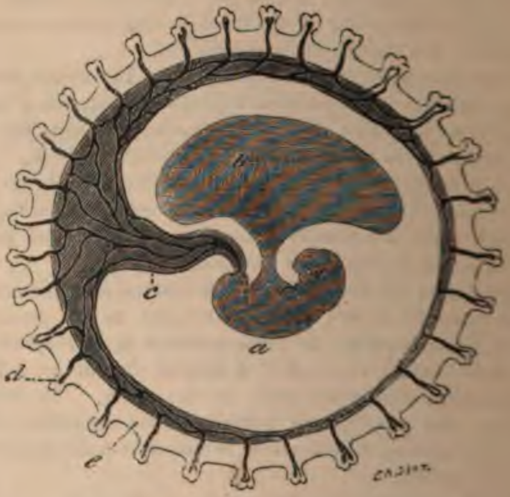


Fig. 256.—Diagram of an embryo, showing the relationship of the vascular allantois to the villi of the chorion. (Cadiat.)

a, Lies in cavity of the amnion under the embryo. *b*, Yolk-sac. *c*, Allantois. *d*, Vessels of the Allantois dipping into the villi of the chorion. *e*, Chorion.

remains as the urinary bladder, and the rest forms a fibrous cord which runs from the apex of the bladder to the umbilicus, and is known as the *urachus.*

(4) *The Chorion* is the external covering of the ovum. At first it consists simply of the zona pellucida or vitelline membrane, and then it is called the primitive chorion. Later, however, it is supplemented by the part of the somatopleure removed from the embryo in the process of forming the amnion. This blends with the primitive chorion and strengthens it, and while lying beneath the zona pellucida, receives the name of the subzonal membrane. The chorion at first is a smooth membrane, but villous processes early grow out from it. These villi are chiefly developed at

its upper part, where they aid in the formation of the fœtal placenta.

The allantois, when it has spread over the chorion, becomes blended with this membrane, and fills the villous processes with the blood-vessels it contains.

The Placenta.

The placenta is a most important organ to the mammalian embryo. It conveys not only nourishment but also oxygen from the maternal blood to that of the fœtus. It is, of course, necessary that the animals whose ova do not contain large stores of food, should in some way provide the substances necessary for the life of their embryo, and it is by means of the placenta that this is brought about. The embryo of oviparous animals does not require a placenta for its nutrition, since inside the egg is a large store of highly nutritious albuminous and fatty materials; the shell is pervious to air, and the chick's blood can in the allantois be oxydised by the air directly. A bird's egg contains in itself all the necessaries which the placenta supplies, and when impregnated only requires the heat of the mother's body to develop a chick.

While an ovum is descending the Fallopian tube, the mucous membrane of the uterus becomes turgid, and, as before mentioned, if the ovum be unimpregnated it is cast out of the body, part of the substance of the lining membrane of the uterus is desquamated and discharged with a fluid largely composed of blood. This takes place approximately every four weeks, and hence is called menstruation. If, however, the ovum be impregnated the mucous membrane of the uterus not only becomes turgid, but its cells proliferate, and considerable thickening of the tissue takes place. The mucous membrane is then called the *decidua.* When the ovum reaches the uterus it ordinarily becomes embedded in that part of the decidua which occupies the fundus of the uterus. The decidua here grows excessively, and becomes much thickened, and on either side of the ovum a projection is sent from the decidua which meets below the ovum, and completely encircles it.

To the membrane lining the general cavity of the uterus the name *decidua vera* is given, whilst that part lining the fundus, to which the ovum is attached, is called the *decidua serotina,* its processes surrounding the ovum receiving the name of the *decidua reflexa.*

The placenta is developed from two sources, one arising from the *membranes of the* fœtus, and the other belonging to the mother.

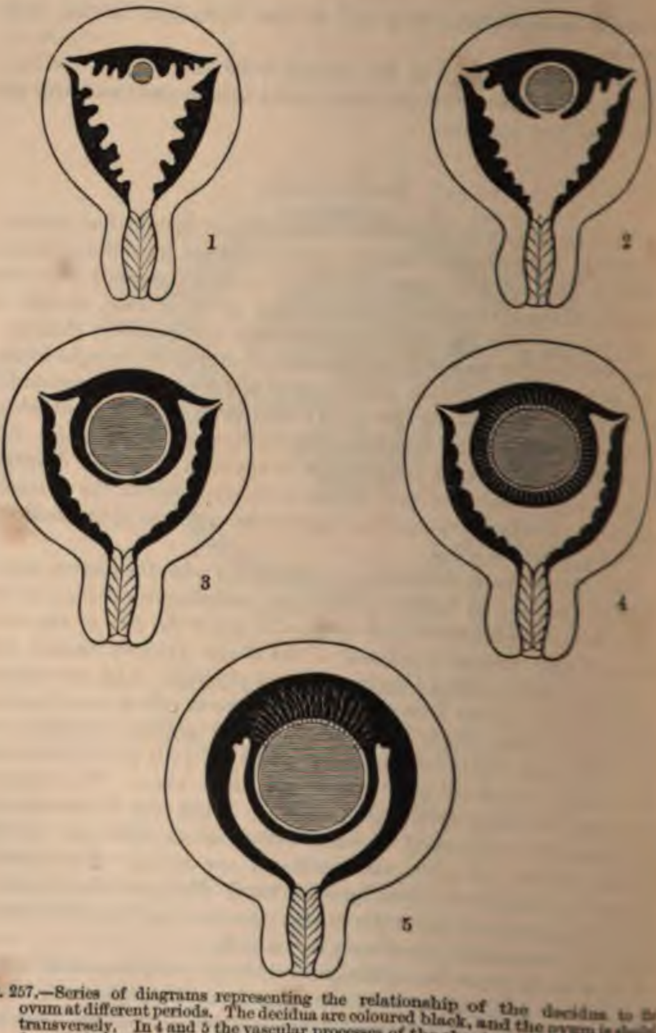


Fig. 257.—Series of diagrams representing the relationship of the decidua to the ovum at different periods. The decidua are coloured black, and the ovum is shaded transversely. In 4 and 5 the vascular processes of the chorion are figured (copied from Dalton).

1. Ovum entering the congested mucous membrane of the fundus—decidua serotina.
2. Decidua reflexa growing round the ovum.
3. Completion of the decidua around the ovum.
4. General growth of villi of the chorion.
5. Special growth of villi at placental attachment, and atrophy of the rest.

Relation of the fœtal to maternal placentæ.—The maternal part is formed from the decidua serotina, which becomes much thickened and very vascular where the placenta is attached. The fœtal placenta is derived from the chorion, which sends out a number of finger-like processes, which sub-divide, and into which the allantois, as it spreads over the chorion, sends prolongations. The mesoblastic layer of the allantois gives rise to the

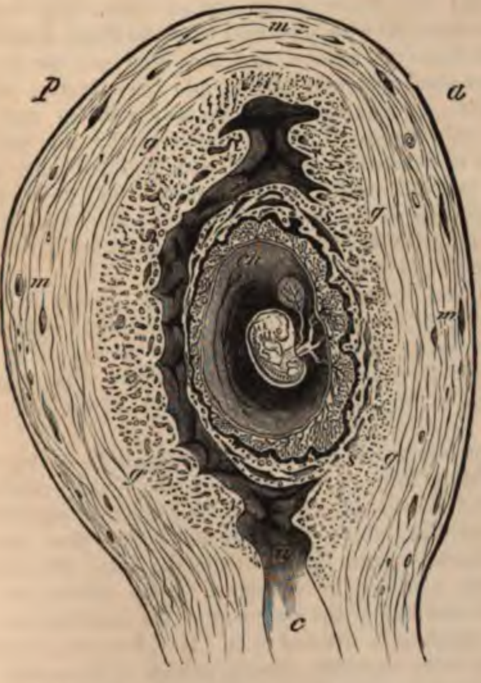


Fig. 258.—Antero posterior section through a gravid uterus and ovum of five weeks (semi-diagrammatic). (Allen Thomson.)

a. Anterior wall of uterus.
p. Posterior wall of uterus.
m. Muscle substance.
g. Glandular layer.
ss. Decidua serotina.
r. Decidua reflexa.
v. Decidua vera.
ch. Chorion.
u.u. Uterine cavity.
c. Cavity of the cervix.

capillaries which are in these processes. The capillaries spring from the branches of the umbilical arteries which pass along the umbilical cord to reach the chorion. The vessels of the decidua serotina or maternal placenta end in large sinuses, lined by endothelial cells. The blood is carried to these sinuses by the uterine arteries, and from them by the uterine veins. The walls of the sinuses are provided with unstriped muscular tissue, which can close the inlets from the arteries, and thus shut out the blood. The villi of the fœtal placenta, dipping into these uterine sinuses, are covered with a single layer of thin scaly cells, so that the fœtal blood is only separated from the maternal by the walls of the capillaries and these thin cells, and thus the interchange of nutrient materials and gas readily go on between them ; it is very similar to the conditions of the lung alveoli, where the blood is separated from the air with which it interchanges gases by the cells of the capillary wall and of the lung alveolus.

Though the capillaries of the fœtus are in such close relation to the blood of the mother, it must be distinctly understood that there is no direct communication between the vessels of the fœtus and those of the mother, and therefore it is not possible to inject the vessels of the mother through those of the fœtus, or *vice versâ*.

The nutrient materials from the maternal blood together with oxygen diffuse through the walls of the fœtal capillaries, the effete matter, on the other hand, passing from the capillaries to the blood in the veins which surrounds and bathes these vessels. The placenta increases with the growth of the fœtus till shortly before birth, when it is said to undergo a certain amount of degeneration. It is cast out of the uterus after the expulsion of the fœtus with the membranes attached to it. It is, however, only the superficial layer of the maternal placenta (which is intimately connected with the fœtal placenta) that is cast off, the deeper layer remaining in the uterus, and undergoing various changes during the reduction of this organ to its normal size.

After ligature of the umbilical cord, the intimate relationship of the maternal and fœtal circulations cease, and it is thought that this causes the inlets of the uterine sinuses to contract, so that when the placenta separates from the uterine walls, the arterioles leading to the sinuses are contracted and possibly occluded with clots. The uterine blood current is thus prevented from escaping into the uterine cavity after parturition, and causing profuse hæmorrhage.

The uses of the placenta may be briefly summed up as—

(1) *Alimentary*, as it supplies the place of the alimentary canal.

(2) *Respiratory*, as it performs the function of the lungs.

(3) *Excretory*, as it does duty for the kidneys and some other excretory organs.

CHAPTER XXXVIII.

DEVELOPMENT OF THE SPECIAL SYSTEMS.

DEVELOPMENT OF THE VERTEBRAL AXIS.

THE earliest evidence of the differentiation of the blastoderm consists in the appearance of the *primitive streak* which forms the first sign of the embryo. This is a line which appears near what is to be the tail end of the embryo, and runs forwards. This primitive line or streak is due to the thickening of the mesoblast, and it becomes converted into a groove by a depression appearing in its centre, forming the *primitive groove*. This extends in a forward direction, but never reaches the head fold of the embryo, which, in the chick, appears a few hours after the formation of the primitive groove.

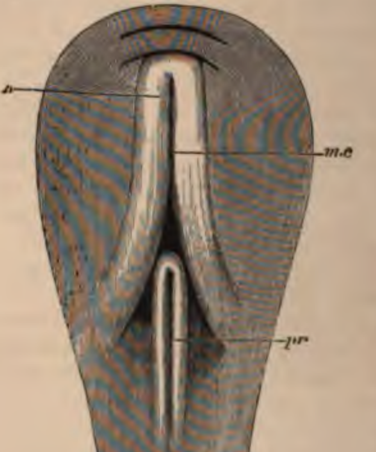


Fig. 250.—View of the area pellucida of a chick of eighteen hours seen from above. (Foster and Balfour.)

A. Medullary folds.
mc. Medullary groove.
pr. Primitive streak and groove.

In front of the primitive groove, and stretching backwards to overlap it at the sides, arise two folds of the epiblast, called the laminæ dorsales or the *medullary folds*.

These are elevations of the epiblast, beneath which the mesoblast is thickened. They arise in front, where they are joined immediately behind the head fold, whilst posteriorly they diverge, and passing on either side of the primitive groove, gradually become lost.

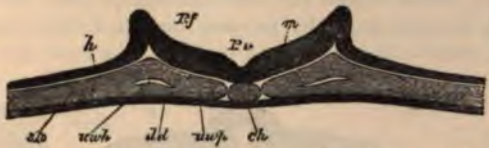


Fig. 260.—Transverse section of the embryo of a chick at the end of the first day. (Kölliker.)

sp. Mesoblast.
d.d. Hypoblast.
m. Medullary plate.
h. Epiblast.
Pv. Medullary groove.
Rf. Medul lary fold.
ch. Chorda dorsalis.
uwp. Proto-vertebral plate.
uwh. Division of mesoblast.

Between the two folds is a furrow lined by epiblast, which is called the *medullary groove.*

The medullary folds growing upwards, turn in towards one another, and eventually coalesce at their line of meeting, converting the medullary groove into a channel—the *medullary canal;* this union of the folds takes place from before backwards.

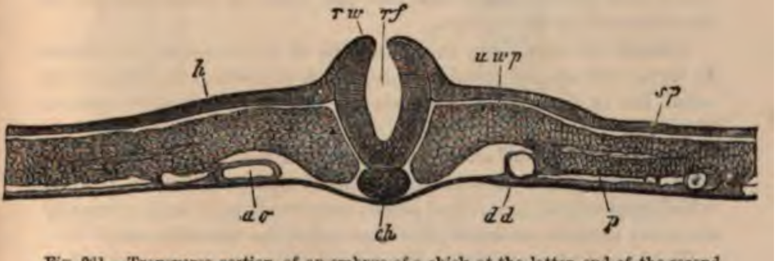


Fig. 261.—Transverse section of an embryo of a chick at the latter end of the second day. (Kölliker.)

rw. Medullary fold.
rf. Medullary groove.
h. Epiblast.
ao. Aorta.
dd. Hypoblast.
p. Pleuroperitoneal cavity.
sp. External plate of mesoblast dividing.
uwp. Proto-vertebral plate.

The medullary canal thus formed lies in the axis of the embryo on the uncleft mesoblast; it is covered in superficially by several layers of epiblastic cells, which also line its walls. The canal is *the earliest* representative of the nervous centres, and eventually becomes the brain and spinal cord. The front part of the canal, when completely closed in, becomes dilated into a bulb, thus forming the earliest indication of the brain. The hind part of the medullary groove remains unclosed considerably later than the front part. It, however, gradually becomes converted into a canal at the tail end, and as it extends backwards it obliterates the primitive streak and groove, which are lost, and take no permanent part in the formation of the embryo.

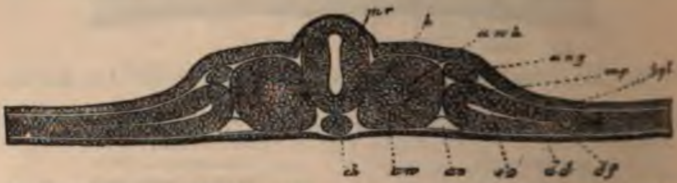


Fig. 202.—Transverse section through the embryo of a chick on the second day when the medullary canal is closed. (Kölliker.)

mr. Medullary canal.
h. Epiblast.
uwh. Cavity of protovertebra *uw.*
ung. Wolffian duct.
mp. Mesoblast dividing into
hpl. Somatopleure.
df. Splanchnopleure.
sp. Pleuroperitoneal cavity.
dd. Hypoblast.
ch. Notochord.

Beneath the medullary canal the cells of the mesoblast are altered to form a rod-shaped cellular body, which following the line of the canal lies in the axis of the embryo; this is the *chorda dorsalis* or *notochord.*

Supporting the medullary canal on either side of the chorda dorsalis are masses of mesoblast, somewhat quadrangular in section, which are termed the *vertebral plates;* continuous with these externally are other thinner masses of mesoblast called the *lateral plates.*

The lateral plates become divided into an upper part or *somatopleure,* which is in close relationship to the epiblast, and a lower part, the *splanchnopleure,* which is next to the hypoblast; the space between these being the *pleuroperitoneal cavity.* The vertebral plates become separated from the lateral plates by a longitudinal partition, so that on either side of the neural canal is a mass of undivided mesoblast extending laterally towards the divided mesoblast.

In each vertebral plate there appear transverse vertical interruptions at definite intervals which split the plate up into a number of quadrangular blocks of mesoblast, known as the *protovertebræ;* the number of these corresponds to the number of vertebræ of the animal.

These protovertebræ become subdivided by transverse fissures into external parts, the *muscle plates*, which form eventually the dorsal and other muscles, and internal parts which become the permanent vertebræ.

From these inner portions processes of mesoblast grow upwards over the medullary canal to meet with processes from the protovertebræ of the opposite side. Mesoblastic tissue also grows inwards between the medullary canal and the notochord, and between the notochord and the subjacent hypoblast.

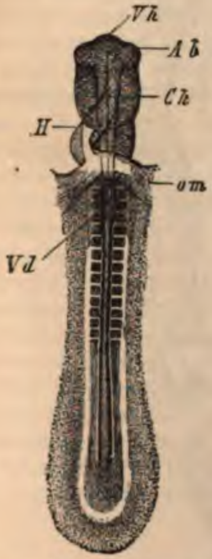


Fig. 263.—Embryo chick at the end of the second day seen from below. (Kölliker).

Vh. Forebrain.
Ab. Optic vesicles.
Ch. Notochord.
H. Heart.
om. Omphalo-mesenteric veins.
Vd. Lower opening of foregut.

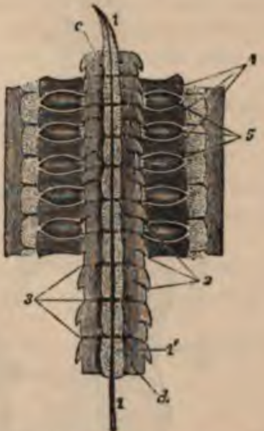


Fig. 264.—Division of the vertebral column of a chick. (Kölliker after Remak.)

1. Notochord.
2. Points of separation of the original protovertebræ.
3. Points of division of the permanent vertebræ.
4. Arches of the vertebræ.
5. Spinal ganglia.
c. Body of first cervical vertebra.
d. One of the lower vertebræ.

These projections beneath the notochord meet with projections from

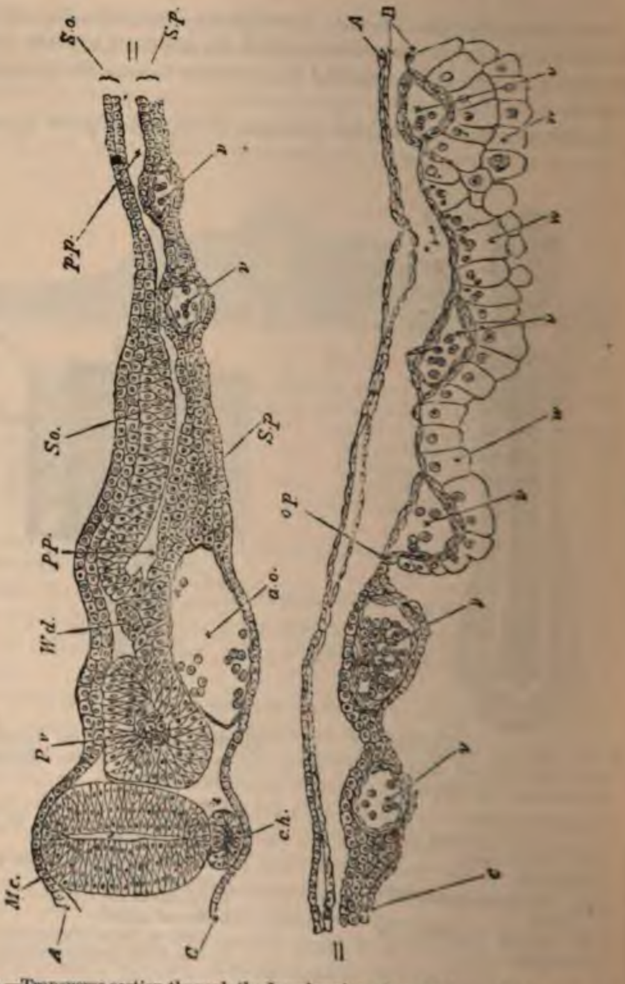


Fig. 265.—Transverse section through the dorsal region of an embryo chick of forty-five hours. (Foster and Balfour).

- *A.* Epiblast.
- *M.c.* Medullary canal.
- *P.v.* Proto-vertebræ.
- *W.d.* Wolffian duct.
- *p.p.* Pleuroperitoneal cavity.
- *S.o.* Somatopleure.
- *S.p.* Splanchnopleure.
- *v.v.* Vessels.
- *a.o.* Aorta.
- *B.* Mesoblast.
- C. Hypoblast.
- o.p. Line of union of opaque and pellucid areas.
- w. Spheres of the white yolk.

a mass of the mesoblast, which lies between the protovertebræ and the cleft mesoblast, which is known as the intermediate cell mass.

The portions of the protovertebræ above the medullary canal form the arches of the vertebræ; from those surrounding the notochord the bodies of the vertebræ are developed.

The outer part of each protovertebra divides into an anterior or pre-axial part, from which arises the ganglion of a spinal nerve, and into a posterior or post-axial part.

After this the original lines of separations between the protovertebræ disappear, and the spinal column is fused into a cartilaginous mass. New segmentation now appears in the centre of each original protovertebra, midway between the primary divisions. Thus the vertebral column is divided into a number of component parts, each of which is destined to become a permanent vertebra.

The vertebræ do not then correspond to the original protovertebræ, but rather to the posterior half of that which lay in front of the primary division joined to the anterior half of the one behind. The ganglia of the spinal nerves, therefore, by this arrangement, instead of belonging to the front of the vertebra become joined to the posterior part of the vertebra, to which they belong.

The notochord atrophies with ossification of the vertebræ, and finally is represented only by a mass of soft cells in the centre of an intervertebral disc.

In connection with the vertebræ in the dorsal region, processes grow horizontally, these are the rudiments of the ribs.

DEVELOPMENT OF THE CENTRAL NERVOUS SYSTEM.

Spinal Cord.

Soon after the closure of the medullary or neural canal at its anterior or cranial end, it is dilated in this region into three vesicles known as the first, second, and third cerebral vesicles, from which the brain is developed. The spinal cord is formed from the part of the medullary canal which lies over the chorda dorsalis. The medullary canal is lined by columnar cells derived from the epiblast, which, shortly after they are shut off from the general epiblast, develop at the sides of the canal, so as to narrow the lumen of the tube by the increase in thickness of its sides. The upper and lower parts of the canal do not, however, become thickened. The lateral walls approximate to the centre, decreasing laterally the lumen of the *canal*, which becomes narrow in the middle with a dilatation above and below. The lateral walls of the canal, the approximated, unite in their centre, and convert the medullary canal into two separate tubes, a dorsal and a ventral.

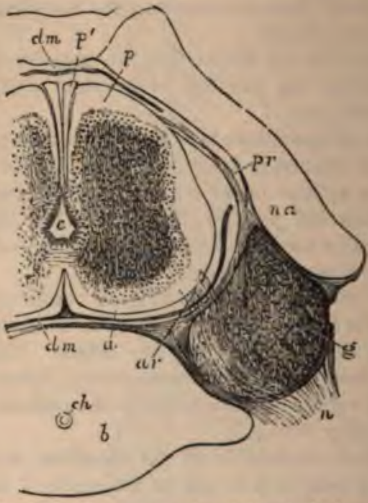


Fig. 266.—Transverse section of the spinal column of the human embryo of from nine to ten weeks. (Kölliker.)

dm. Dura mater.
p'. Columns of Goll.
p. Posterior column.
pr. Posterior root.
na. Arch of vertebra.
g. Ganglion of a spinal nerve.
a. Anterior column.
ar. Anterior root.
ch. Notochord.
b. Body of the vertebra.
n. Spinal nerve.
c. Central canal.
e. Epithelium of canal.

The lower or ventral tube of the divided canal becomes the central canal of the spinal cord, and the columnar cells of the epiblast form a lining of ciliated columnar epithelium.

The epiblast at the lower part of the canal become converted into the anterior grey columns, in connection with which arise the anterior roots of the spinal nerves; whilst at the upper part the posterior grey columns are formed in connection with the posterior roots of the spinal nerves and their ganglia.

The white columns are thought by some authors to be derived from the mesoblast surrounding the canal, but by others they are assigned to the epiblast.

The upper or dorsal canal becomes converted into a fissure by the absorption of its roof, and is thus changed into the posterior fissure of the spinal cord.

The anterior fissure is formed by the downgrowth of the anterior columns, which diverge, leaving between them an interval which becomes occupied by the pia mater.

The commissures are not formed between the lateral halves of the cord until later. The grey commissure appears first.

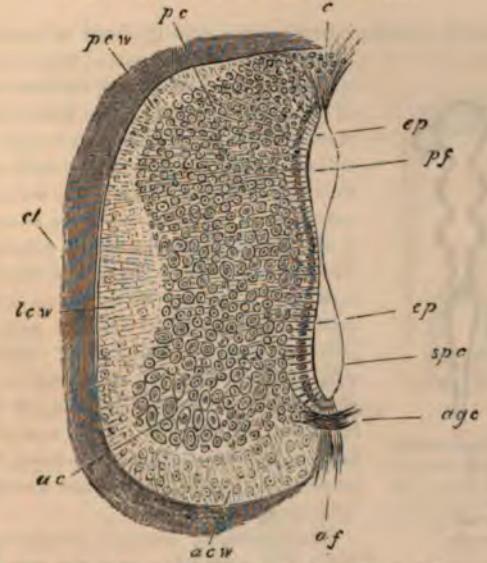


Fig. 267.—Transverse section of the spinal cord of a chick of seven days. (Foster and Balfour.)

ep. Epithelium lining the medullary canal. *pf*. Part of the cavity of the medullary canal which becomes the posterior fissure. *spc*. Permanent medullary tube or central canal of the spinal cord. *agc*. Anterior grey commissure. *af*. Anterior fissure, not yet well formed. *c*. Tissue filling in the upper part of the posterior fissure. *pc*. Cells forming the posterior grey matter. *pcw*. Posterior white column. *ct*. Mesoblast surrounding the spinal cord. *lcw*. Lateral white column. *acw*. Anterior white column. *ac*. Cells forming the anterior grey matter.

The Brain.

Anterior cerebral vesicle.—As already mentioned, the brain is formed from the primitive neural canal, the anterior part of which becomes dilated into three little swellings called the anterior, middle, and posterior cerebral vesicles. From the anterior, or first cerebral vesicle, at an early period spring two processes, which become the optic vesicles. These ultimately become developed into the retina and other nervous parts of the eye, with the history of which the changes occurring in them will be described.

The optic vesicles are displaced downwards by two processes growing forwards from the anterior cerebral vesicle, which becomes divided into two parts, the anterior of which is subsequently developed into the cerebral hemispheres and the olfactory lobes, while the hinder part receives the name of *thalamencephalon*.

The cavity of the thalamencephalon opens behind into the cavity of the middle cerebral hemisphere, and in front it communicat with the hollow rudiments of the cerebral hemispheres, and eventually it becomes the cavit of the third ventricle. The floor of the thalamencephalon is ultimately developed into th optic chiasma and part of the optic nerves, a well as the infundibulum. The latter comes i contact with a process from the mouth, whi is ultimately changed into the pituitary bod The anterior part of the roof of the thalamencephalon becomes very thin, and its place i finally occupied by a vascular plexus, whi persists in the roof of the third ventricle (choroid plexus). The pineal gland—a pecul outgrowth, of unknown function—is develope from the posterior part of the roof of the thalamencephalon and from its sides, which become extremely thickened, are developed th *optic thalami.*

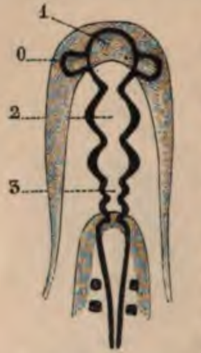


Fig. 268.—Diagram of the cerebral vesicles of the brain of a chick at the second day. (Cadiat.) 1, 2, 3, Cerebral vesicles. 0. Optic vesicles.

The primitive cerebral hemispheres fi appear as two lobes growing out from th front of the anterior part of the first cerebral vesicle. The floor o these lobes thickens to give rise to the *corpora striata*, and the ro

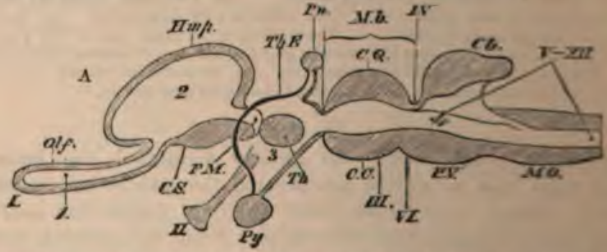


Fig. 269.—Diagram of a vertical longitudinal section of the developing brain of a vertebrate animal, showing the relation of the three cerebral vesicles to the differen parts of the adult brain. (Huxley.)
Olf. Olfactory lobes. *Fm.* Foramen of Monro. *Cs.* Corpus striatum. *Th.* Optic thalamus. *P.n.* Pineal gland. *M.b.* Mid brain. *Cb.* Cerebellum. *Mo.* Medulla oblongata. *Hmp.* Central hemispheres. *Th.E.* Thalamencephalon. *Py.* Pituitary body. *CQ.* Corpora Quadrigemina. *C.C.* Crura cerebri. *P.V.* Pons Varoli *I.—XII.* Regions from which spring the cranial nerves. 1. Olfactory ventric 2. Lateral ventricle. 3. Hind ventricle. 4. Fourth ventricle.

develops into the hemispheres proper. The cavities of these lobe become the lateral ventricles, and are connected by means of th foramen of Munro, which at the earlier periods is very wide, but su sequently becomes narrowed to a mere slit. The cerebral hemisph are separated by the ingrowth of a septum, which is ultimately formed into the *falx cerebri.* The hemispheres are then greatly enlarged in the backward direction, so that they quite overlap the thalamencephalon and the parts developed from the middle cerebral vesicle. The corpus callosum is subsequently formed by the fusion of the juxtaposed parts of the hemispheres.

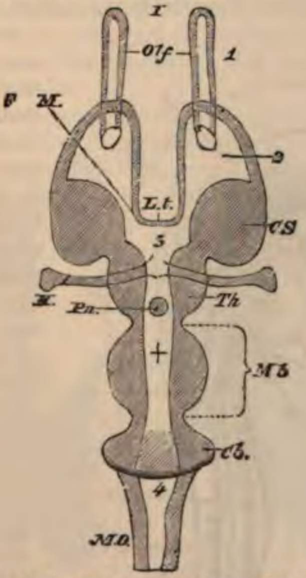


Fig. 270.—Diagram of a horizontal section of a vertebrate brain. (Huxley.)
Olf. Olfactory lobes. *Lt.* Lamina terminalis. *Cs.* Corpus striatum. *Th.* Optic thalamus. *P.n.* Pineal gland. *Mb.* Mid brain. *Cb.* Cerebellum. *Mo.* Medulla oblongata. 1. Olfactory ventricle. 2. Lateral ventricle. 3. Hind ventricle. 4. Fourth ventricle. + Iter a tertio ad quartum ventriculum.

From the anterior part of the cerebral hemispheres arise two prolongations, which develop into the olfactory bulbs, these grow forwards, and soon lose their cavities which at first communicated with those of the ventricles.

Middle cerebral vesicle.—By the cranial flexure the brain is bent at the junction of the first and second cerebral vesicles, the first cerebral vesicle is thus turned downwards, leaving the second vesicle as the most anterior part of the brain.

The upper walls of the second cerebral vesicle are developed into the corpora quadrigemina.

The cavity of this vesicle persists as a narrow channel, and forms *a communication* between the third ventricle in front and the

fourth ventricle behind, and receives the name in the adult br
of the *iter a tertio ad quartum ventriculum*. The crura cerebri ar
from the lower wall of this middle vesicle.

The *third cerebral vesicle* is divided into an anterior and a posteri
part. From the upper part of the anterior division arises the ce
bellum, and from its lower part the pons Varolii.

The posterior division gives rise to the medulla oblongata.

The cavity of th
vesicle is called th
fourth ventricle. It
continuous with th
central canal of th
spinal cord. Its upp
wall is thinned a
forms the valve Vie
sens. It communica
with the subarachn
space through the fo
men of Majendie.

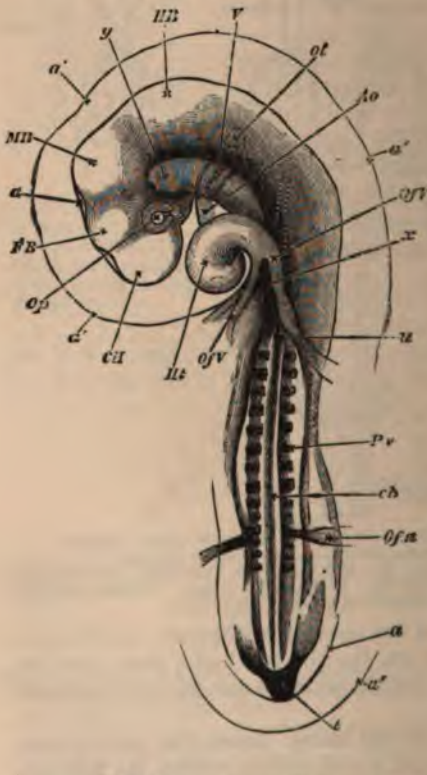


Fig. 271.—Chick on the t
day seen from beneat
a transparent object,
head being turned to
side. (Foster and Balfo

a'. False amnion.
a. Amnion.
CH. Cerebral hemisphere
F.B., *M.B.*, *H.B.*, Ante
Middle, and Posterior c
bral vesicles.
op. Optic vesicle.
ot. Auditory vesicle.
ofv. Omphalo - mesen
veins.
Ht. Heart.
Ao. Bulbus arteriosus.
Ch. Notochord.
Of.a. Omphalo-mesent
arteries.
Pv. Proto-vertebræ.
x. Point of divergence of
splanchnopleural fol
y. Termination of the f
gut, V.

THE ALIMENTARY CANAL AND ITS APPENDAGES.

When the blastoderm is bent at its anterior extremity to form
cephalic fold, it closes in and forms the anterior boundary of a s
canal, the upper wall of which is formed by the general bla
derm, and its lower wall by that part of the splanchno

which runs backwards, leaving the somatopleure, to form the pleuro-peritoneal space. It then turns forwards to meet with the uncleft mesoblast, forming the wall of the yolk sac, which communicates freely with this rudimentary part of the alimentary tract.

This canal becomes closed in for a considerable extent, and is then called the *fore-gut*. It is the precursor of the pharynx, the lungs, the œsophagus, the stomach, and the duodenum. The mouth, which at this period is unformed, is developed later by an involution of the epiblast and the removal of the tissue between the fore-gut and the buccal cavity.

The tail fold, in a somewhat similar manner, shuts off a canal called the *hind-gut*, which becomes developed into the posterior part of the alimentary canal. This hind-gut until the further development of the bladder, &c., is in connection with the allantois which arises as a bud from the lower part of the rudimentary hind-gut.

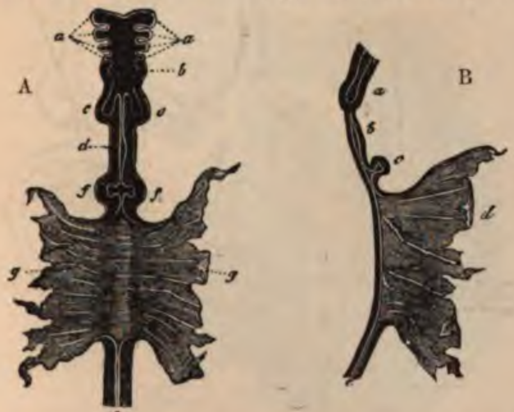


Fig. 272.—Alimentary canal of an embryo whilst the rudimentary mid-gut is still in continuity with the yolk sac. (Kölliker after Bischoff.)

A. View from below.
a. Pharyngeal plates.
b. The pharynx.
c.c. Diverticula forming the lungs.
d. The stomach.
f. Diverticula of the liver.
g. Membrane torn from the yolk sac.
h. Hind-gut.

B. Longitudinal Section.
a. Diverticulum of a lung.
b. Stomach.
c. Liver.
d. Yolk sac.

Between these two canals an intermediate one is formed by the splanchnopleure of the mesoblast, which, at a distance from its origin, *becomes constricted*, and shuts off an upper canal, the mid-gut, from a lower larger organ, the yolk sac, the connection between the tw forming the *ductus vitello-intestinalis.*

Thus the primitive alimentary canal consists of an anterior and a posterior canal, which are closed below, and a canal intermedia between these, which opens at its lower surface into the yolk sac.

As the placental circulation becomes more and more developed, so the yolk sac shrinks and atrophies, until at last it is represented by a fold of tissue connected with the primitive intestine. The ductus vitello-intestinalis accordingly becomes obliterated, and thus the mid-gut is closed at its lower aspect.

The primitive intestine placed at the inferior aspect of the embryo, just below the protovertebræ, is lined internally by hypoblast, and covered externally by mesoblast. The cephalic or anterior extremity of the canal is formed by uncleft mesoblast; the rest of the canal is formed by the splanchnopleural layer of the mesoblast.

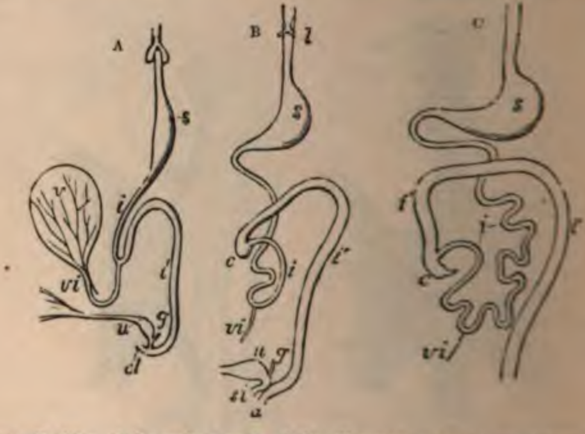


Fig. 273.—Position of the various parts of the alimentary canal at different stag A. Embryo of five weeks; B. Of eight weeks; C. Of ten weeks. (Allen Thomson.)

l. Pharynx with the lungs.
s. Stomach.
i. Small intestine.
i'. Large intestine.
g. Genital duct.
si. Urogenital sinus.
u. Bladder.
cl. Cloaca.
c. Cæcum.
vi. Ductus vitello intestinalis.
v. Yolk-sac.

A dilatation of a part of the fore-gut gives origin to the primitive stomach; this is quite straight at first, lying below the vertebral column, with which it is connected by mesoblast. After a time the stomach becomes turned to the right side, so that the left the organ comes to lie anteriorly and the right surface posteriorly, the mesoblast connecting it with the vertebral column, being developed into the peritoneal processes of the organ.

The lower part of the fore-gut is of much smaller calibre than the dilated portion forming the stomach; it becomes the duodenum, in connection with which arise two important viscera, the liver and the pancreas.

The mid-gut and hind-gut form the small and large intestines, these being at first one straight tube, of which the small intestine has the larger calibre. The small intestine, as it grows, falls into folds, and the mesoblast connecting it to the vertebral column forms the mesentery.

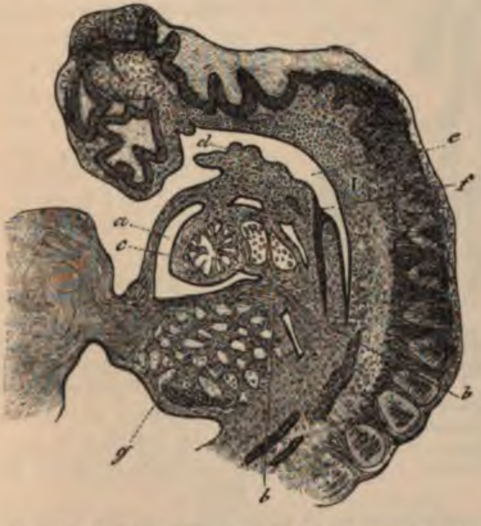


Fig. 274.—Longitudinal section of a fœtal sheep. (Cadiat.)

a. Pericardium.
b. Commencement of Diaphragm.
c. Heart.
d. Branchial arches.
e. Pharynx.
f. Origin of lung.
g. Liver.

The large intestine is at first a straight tube lying to the left of the embryo; it becomes bent, and part of the tube is directed towards the right side; this develops another flexure, the portion of intestine below which grows downwards. Thus that part remaining on the left side forms the rectum, the sigmoid flexure, and the descending colon; whilst that part between the flexures becomes the transver colon, and that on the right side the ascending colon.

The cæcum is developed from the ascending colon, the ileo-cæ valve arising and shutting off the one part of the intestinal ca from the other. The vermiform appendix originates from the inferi extremity of the cæcum, which, owing to its feeble growth, is much smaller calibre than the upper part.

The epithelial lining of the intestines is derived from the hypobla and the muscular, vascular, conne tive tissue, and serous coverings a mesoblastic in their origin.

The liver is developed from tw diverticula of the duodenum, in co nection with which arise cylind of cells. The hypoblast develo into the liver cells and the ce lining the ducts, the mesobla furnishing the vascular and co nective tissue parts of the org The two diverticula are connect by a transverse piece, and form th right and left lobes of the liver.

The process connecting the liv to the duodenum forms the comm bile duct, and from this the gall bla der is developed as an outgrowth.

The vessels of the embryo, whi are in relation to the liver, w be described under the vascu system.

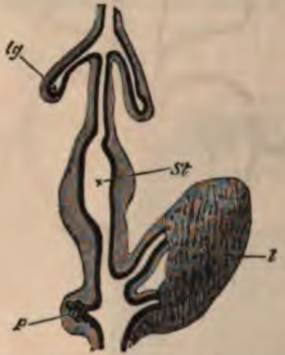


Fig. 275.—Diagram of the alimentary canal of a chick at the fourth day. (Foster and Balfour, after Götte.)

lg. Diverticulum of one lung.
St. Stomach.
l. Liver.
p. Pancreas.

The pancreas arises as an outgrowth from the duodenum, its co stituent parts originating in a manner similar to those of the liver.

The spleen is derived from the mesoblast, and is developed in o of the peritoneal processes of the stomach.

The lungs are developed in connection with the œsophagus, which they are early outgrowths.

The canal of the fore-gut at a certain point becomes laterall constricted, its transverse section presenting an hour-glass shap consisting of an upper, and a lower dilated portion, united by central constricted neck. The lower of these cavities becomes su divided by the outgrowth of the lateral portions and the upgrow of a part of the lower wall which forms a central septum, so that fore-gut comes to be composed of an upper undivided tube, giving off two appendages.

These appendages consist of hypoblastic tissue, and as they grow into the surrounding mesoblast they divide and sub-divide, until at last they come to consist of very minute tubules, which terminate in dilated extremities. The undivided canal forms the permanent trachea, the appendages the main bronchi, whilst their minute subdivisions are the bronchioles, which terminate in the dilated alveoli.

The hypoblast forms the delicate lining membrane of the air passages, and the mesoblast gives rise to the supporting tissue holding them together, as well as to the blood-vessels, the muscular, cartilaginous, and connective tissue of the bronchial tubes.

The pleuræ surrounding the lungs are like the other serous membranes, also mesoblastic in their origin.

Genito-urinary Apparatus.

In the interval between the protovertebræ and the cleavage of the mesoblast into its somatopleural and splanchnopleural layers, there appears a mass of cells, which arrange themselves into the form of a ridge. This ridge, which lies beneath the epiblast, becomes hollow, and thus a tube is produced, which is called the *Wolffian duct*.

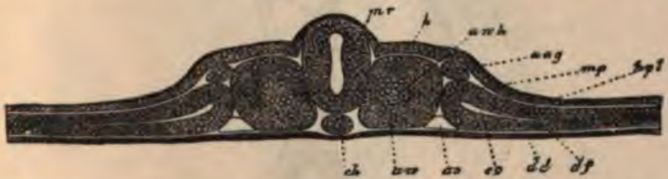


Fig. 276.—Transverse section through the embryo of a chick on the second day where the medullary canal is closed. (Kölliker.)

mr. Medullary canal.
h. Epiblast.
uwh. Cavity of protovertebra *uw*.
ung. Wolffian duct.
mp. Mesoblast dividing into
hpl. Somatopleure.
df. Splanchnopleure.
sp. Pleuroperitoneal cavity.
dd. Hypoblast.
ch. Notochord.

From this tube diverticula arise, which extend into the surrounding mesoblast; they are tubular, and communicate with the central duct, whence they arise. The processes become twisted, and at their extremities the neighbouring mesoblast undergoes differentiation, and forms vascular capsules corresponding in structure to the *Malpighian corpuscles*. This part of the Wolffian duct, which has acquired a glandular structure, is the *Wolffian body* or primiti kidney of the embryo, whilst the Wolffian duct corresponds to th primitive ureter.

The epithelium lining the interval between the somatopleure an splanchnopleure (pleuroperitoneal cavity), close to their origin fro the uncleft mesoblast, becomes columnar in character. It receive the name of the *germinal epithelium*. An involution of this take

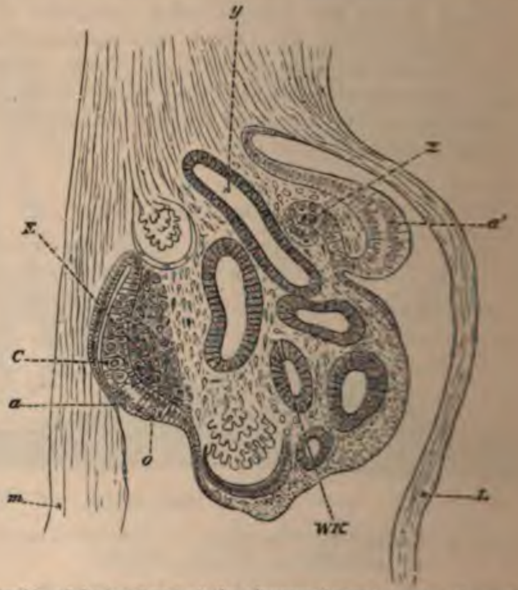


Fig. 277.—Section of the inner part of the pleuroperitoneal cavity through the of the genito-urinary organs. (Waldeyer.)

L. Somatopleure.
m. Splanchnopleure.
a. Germinal epithelium.
C, *o*. Primitive ova.
E. Mesoblast forming the ovary.
WK. Wolffian body.
y. Wolffian duct.
a'. Epithelium giving rise to the of Müller *z*.

place into the mesoblast, just below the somatopleure, and becom shut off, and forms a hollow cylinder.

By this means a second duct is formed in close relation to th first; this is the *Müllerian duct*. This duct is developed from befo backwards.

According as the embryo is a male or a female, so one or th of these ducts develops. In the male the Wolffian duct remains as the vas deferens, and the Müllerian duct becomes atrophied. In the female, on the other hand, the Müllerian duct forms the organs for the conveyance of the ova out of the body, and the Wolffian duct is represented by a rudimentary structure near the ovary.

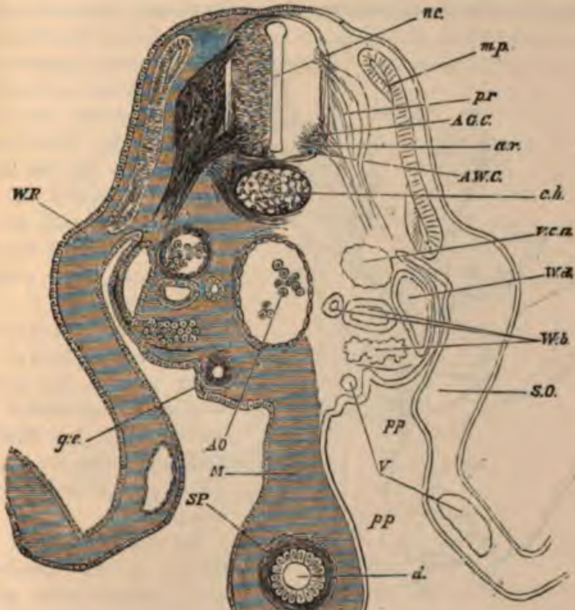


Fig. 278.—Transverse section through the lumbar region of an embryo chick at the end of the fourth day. (Foster and Balfour.)

W.R. Wolffian ridge.
g.e. Germinal epithelium.
A.O. Dorsal aorta.
M. Mesentery.
SP. Splanchnopleure.
d. Alimentary canal.
V. Vessels.
m.p. Commencing Müllerian duct.
So. Somatopleure.
W.b. Wolffian body.
W.d. Wolffian duct.
V.c.a. Posterior cardinal vein.
c.h. Notochord.
A.W.C. Anterior white column of spinal cord.
a.r. Anterior root.
A.G.C. Anterior grey column.
p.r. Posterior root.
m.p. Muscle plate.
nc. Canal of spinal cord.

Part, however, of the Wolffian duct in both sexes develops similarly; this, the *metanephros*, corresponds to that part of the duct nearest to the tail end of the embryo. It forms part of the urinary organs, and develops into the permanent ureter and the kidney.

From the metanephros a projection arises, which grows quickly, and opens into the cloaca; this remains as the ureter. From the upper part of the ureter arise small cæcal evolutions, which become convoluted at certain points and surrounded by mesoblast; these canals are the urinary tubules, and at the extremity of each is developed a tuft of vessels, which thus forms a Malpighian corpuscle.

The straight tubes group themselves together at the inner part of the gland, whilst the convoluted tubules, with the Malpighian corpuscles, are aggregated at the periphery of the gland.

At the junction of the ureter to the glandular mass, changes take place by which this tube is split up into several sub-divisions, which are the primitive calices of the kidney, the dilated part of the ureter forming the pelvis.

The testicle arises partly from the germinal epithelium lining the inner extremity of the pleuro-peritoneal cavity, lying close to the splanchnopleure, and partly from the mesoblast surrounding the Wolffian body.

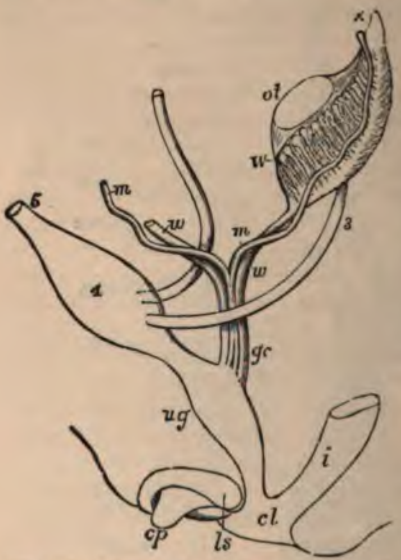


Fig. 279.—Diagram of the genital organs of an embryo previous to sexual distinction. (Allen Thomson.)

W. Wolffian body.
3. Ureter. 4. Bladder. 5. Urachus
gc. Genital cord. *cp*. Clitoris, or penis.
m. Müllerian duct.
w. Wolffian duct. *i*. Intestine.
ug. Urogenital sinus. *cl*. Cloaca.
ls. Part from which the scrotum or the labia majora are developed.
ot. Origin of the ovary or testicle respectively.
x. Part of Wolffian body subsequently developed into the coni vasculosi.

The germinal epithelium, the cells of which are not so well developed as in the female, sends processes into the mesoblast, and these are said to form the spermatic cells, the mesoblast becoming differentiated around them to form the walls of the tubuli seminiferi.

The Wolffian duct, which persists as the vas deferens, aids in forming the testicle, the epididymis being merely a convoluted part of it, and the vas aberrans one of the cæcal tubes in connection with the duct. The coni vasculosi are thought to be formed from some of the tubules of the Wolffian body; they are connected to the testicle by means of a tube which is itself split up into a number of divisions which form the vasa efferentia.

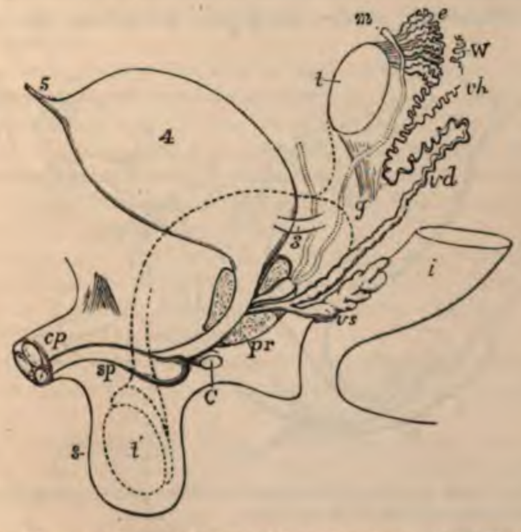


Fig. 280.—Diagram of the sexual organs of the male embryo. (Allen Thomson.)

3. Ureter.
4. Bladder.
5. Urachus.
t. Testicle.
m. Atrophied duct of Müller (hydatid of Morgagni.)
e. Epididymis.
g. Gubernaculum testis.
vs. Vesicula seminalis.
i. Intestine.
pr. Prostate.
W. Organ of Giraldès.
vh. Vas aberrans.
vd. Vas deferens.
C. Cowper's gland.
cp. Penis.
sp. Spongy part of the Urethra.
t'. Position the testicle ultimately assumes.
s. Scrotum.

The Wolffian duct forms, besides the vas deferens, the vesicula seminalis (which is merely a blind diverticulum from its extremity), and terminates in the ejaculatory duct.

The two Müllerian ducts, in the male, join and form a single tube;

this is not further developed, but atrophies, leaving as its representative the sinus pocularis, which is situated in the floor of the prostate. The upper extremities of the Müllerian ducts form the hydatids of Morgagni.

The ovary, like the testicle, is formed from the germinal epithelium, which multiplies and forms a projection close to the Wolffian body. The cells of the epithelium become involuted and surrounded by the uncleft mesoblast, to form ova and Graafian follicles. The glandular part of the ovary thus arises from the germinal epithelium, and its stroma springs from the mesoblast in the neighbourhood of the Wolffian body.

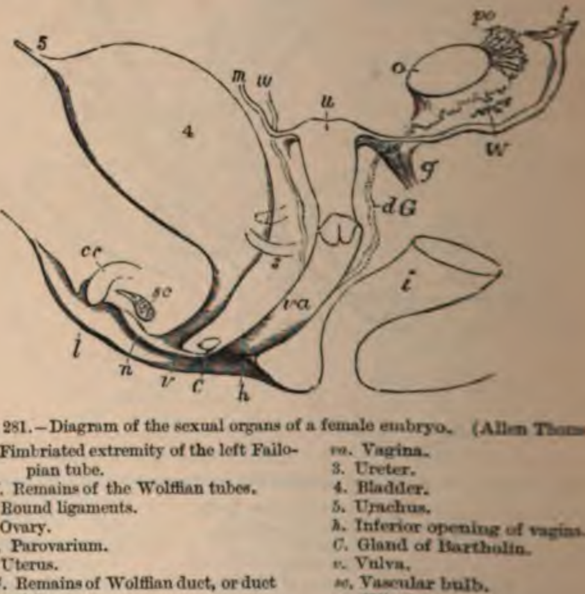


Fig. 281.—Diagram of the sexual organs of a female embryo. (Allen Thomson.)

f. Fimbriated extremity of the left Fallopian tube.
W. Remains of the Wolffian tubes.
g. Round ligaments.
o. Ovary.
po. Parovarium.
u. Uterus.
dG. Remains of Wolffian duct, or duct of Gaertner.
m. Right Fallopian tube cut short.
w. Right obliterated Wolffian duct.
va. Vagina.
3. Ureter.
4. Bladder.
5. Urachus.
h. Inferior opening of vagina.
C. Gland of Bartholin.
v. Vulva.
sc. Vascular bulb.
cc. Clitoris.
n. Nympha.
l. Labium.
i. Rectum.

The ducts of Müller are the precursors of the female genital passages. They approach one another and unite along a certain distance at their lower extremities. Of this united part, the upper end forms the uterus, and the lower the vagina, whilst the united parts of the Müllerian ducts form the Fallopian tubes, which become connected to the ovaries, whilst their cavities remain continuous with the pleuroperitoneal space.

In the female the Wolffian duct and body atrophy, the parovarium being in the adult the representative of the Wolffian body.

The bladder is merely a dilated portion of that part of the allantois which is in immediate connection with the alimentary canal, and the urachus is the narrowed part of the allantois connecting the bladder to the remainder of the allantois which is without the body walls of the fœtus.

While the alimentary canal is in connection with the allantois, the intestinal and genito-urinary passages open into a common cavity at their termination; this is the *cloaca*, and it is in the further development of the embryo that a septum arises, dividing this into an alimentary or anal portion, and an anterior or urinary portion. The septum, dividing the urogenitary from the alimentary portion of the cloaca, forms, externally, the perinæum.

At the aperture of the cloaca an eminence arises which develops into the penis in the male, the clitoris in the female. Around this eminence is a fold of integuments, which forms the labia in the female, the scrotum in the male.

In the female this integumentary covering enlarges much more than the clitoris and covers it in, the urethral orifice opening just below the clitoris.

In the male the urethral orifice at first opens at the base of the penis, but eventually a groove is formed on the under surface of this organ, which becomes converted into a canal, and forms the urethra.

BLOOD-VASCULAR SYSTEM.

In the mammalian embryo this may be appropriately divided into two systems of different dates; the first, or early circulation, which is confined to the yolk sac; and the second, or later circulation, which passes through the placenta.

The Primitive Heart arises from the splanchnopleural layer of the mesoblast, just at the point where this forms the under wall of the fore part of the alimentary canal. When the formation of the folds of the embryo was described, it was stated that the groove of the cephalic fold tended to grow backwards towards the tail end of the embryo. This groove is limited behind by the somatopleural layer of the mesoblast, and posteriorly to this is a cavity formed by the cleavage of the mesoblast, called the pleuroperitoneal cavity. In the early stages of development, the posterior wall of this small cavity is formed by the splanchnopleural layer of the mesoblast. The heart arises at the point at which the splanchnopleure tends to travel forwards to meet the uncleft mesoblast, and thus completes the pleuroperitoneal cavity.

The heart consists at first of a single cylinder, which in the human embryo probably is formed by the coalescence of two primary tubes. At first it has no distinct cavity, but soon the cells of the mesoblast within the mass forming the heart become transformed into blood corpuscles, and thus it is hollowed out. A layer of endothelial cells line the cavity, and become the endocardium.

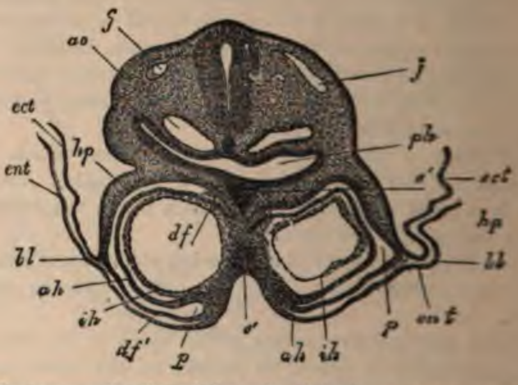


Fig. 282.—Transverse section through the region of the heart of a rabbit's embryo of nine days old. (Kölliker.)

jj. Jugular veins.
ao. Aorta.
ph. Fore-gut.
bl. Blastoderm.
hp. Body wall reflected in *ect*.
ent. Hypoblast.
e'. Prolongation of hypoblast between the two halves of the heart.
ah. Outer wall of the heart.
p. Cavity of the pericardium.
ih. Inner lining of the heart.
ect. Epiblast.
df. Visceral mesoblast.

The primitive heart is connected at its upper end with the two aortæ, and at its lower end with the omphalo-mesenteric veins.

After a time the tube shows signs of division into three parts; the upper part becomes the aortic bulb, next to which is formed the cavity of the ventricle, continuous with which is the auricular space. The tube also, which at first lies in a straight line, now becomes twisted on itself, the auricular part becoming posterior and superior, whilst the ventricle, with the aortic bulb, remains anterior and somewhat below.

Each primitive cavity of the heart is divided into two by the gradual growth of partitions, and thus the four permanent heart cavities are developed.

Externally a notch shows the division of the ventricle into right and left cavities, whilst from the inside of the right wall there grows a projection which sub-divides the ventricle internally. This septum is, however, not at once complete at its upper part, a communication between the right and left sides of the heart remaining for some time above this partition. With the growth of the inter-ventricular septum, the external notch becomes less prominent, but it is permanently recognisable as the inter-ventricular groove.

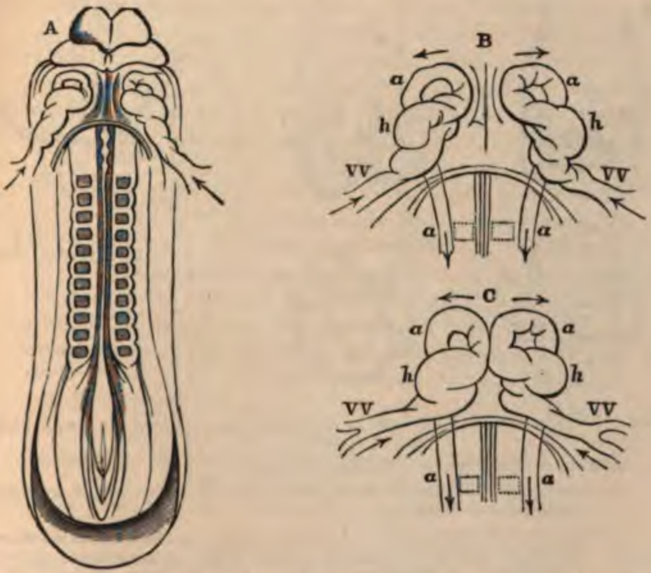


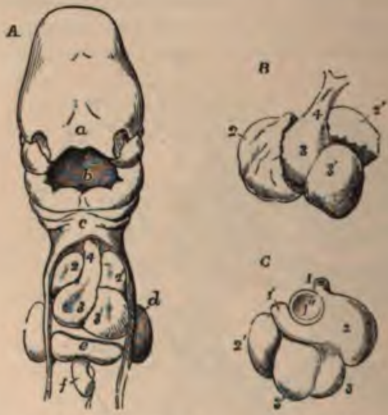
Fig. 283.—Diagrammatic views of the under surface of an embryo rabbit of nine days and three hours old, showing the development of the heart. (Allen Thomson.)

A, View of entire embryo. B, an enlarged outline of the heart of A. C, a later stage of the development of B. *hh*. Ununited heart. *aa*. Aortæ. *VV*. Vitelline veins.

In the auricles a fold develops from the anterior wall, which ultimately unites with a process of later development from the *posterior wall.* This septum is not complete during fœtal life, but is interrupted by an opening leading from one auricle to the other called the foramen ovale.

Simultaneously with the appearance of the posterior process of the septum, another fold arises, which is placed at the mouth of the inferior vena cava, and forms the Eustachian valve.

The aortic bulb likewise, by a projection from the inner wall of the cavity, becomes divided into two canals, the anterior of which



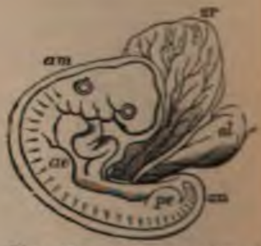


Fig. 285.—Human embryo of about three weeks. (Allen Thomson.)
sv. Yolk sac.
al. Allantois.
am. Amnion.
ae. Anterior extremity.
pe. Posterior extremity.

Fig. 284.—Development of the heart in the human embryo, from the fourth to the sixth week.

A. Embryo of four weeks. (Kölliker after Coste.)

B. Anterior, and C. posterior views of the heart of an embryo of six weeks (Kölliker after Ecker.)

a. Upper limit of buccal cavity. b. Buccal cavity. c. Lies between the ventral ends of the 2nd and 3rd branchial arches. d. Buds of upper limbs. e. Liver. f. Intestine. 1. Superior vena cava. 1′. Left superior vena cava or connection between the left brachio-cephalic vein and the coronary vein. 1″. Opening of inferior vena cava. 2. 2′. Right and left auricles. 3. 3′. Right and left ventricles. 4. Aortic bulb.

remains in continuity with the right ventricle, and the posterior canal is continuous with the left ventricle. The anterior thus becomes the pulmonary artery, and the posterior the permanent aorta.

The primitive circulations of a human embryo may be divided into two, which differ in their time of appearance and in the accessory organs to which they are distributed. Though they may, for the sake of clearness, be described as two independent circulations, they are not strictly so, as they exist for a short time coincidently, and arise in connection with one another from the same heart.

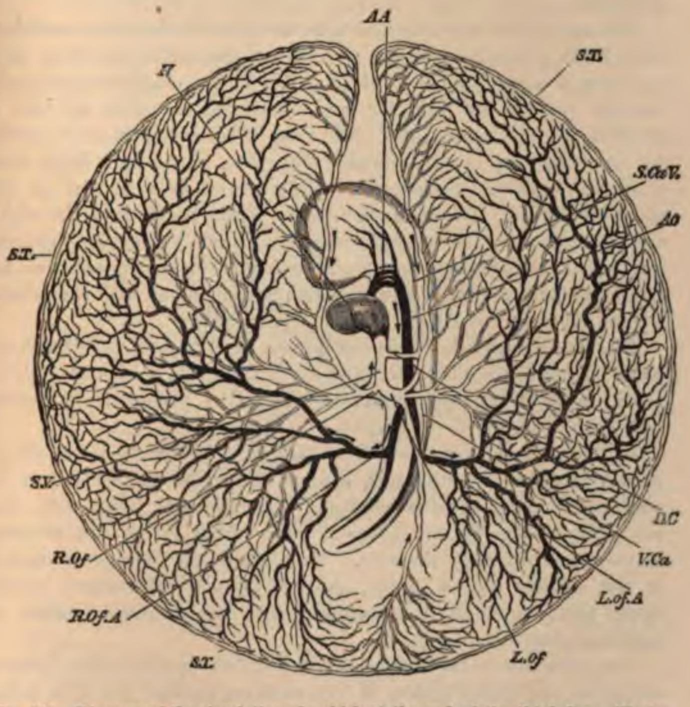


Fig. 286.—Diagram of the circulation of a chick at the end of the third day. (Foster and Balfour.)

H. Heart.
AA. Aortic arches (2nd, 3rd, and 4th.)
Ao. Dorsal aorta.
L.ofA., *R.ofA.* Right and left omphalo-mesenteric arteries.
S.T. Sinus terminalis.
R.of, *and L.of.* Right and left omphalo-mesenteric veins.
S.V. Sinus venosus.
D.C. Duct of Cuvier.
S.Ca. and V.Ca. Superior and inferior cardinal veins.

(*a*) The *earlier or vitelline circulation* is that which is directed to the yolk sac, the embryo obtaining nourishment from the vitellus or yolk; this is, however, an organ of quite secondary importance in the mammalian embryo, and hence this circulation may be better studied in some such animal as the chick, which depends, throughout its embryonic life, on the vitellus for nourishment. In the hu embryo the vitelline circulation is chiefly of importance for few days immediately preceding the development of the placen circulation.

The aortic bulb is continuous with two vessels which run on eit side of the primitive pharynx; these are the aortæ, and from e of them a large branch is given off. These omphalo-mesent arteries pass to the yolk sac, and there become split up into number of small vessels, the blood from them being returned pa by corresponding omphalo-mesenteric veins, partly by a large v running round the periphery of the vascular area known as *sinus terminalis*. The sinus terminalis opens partly into the ri and partly into the left omphalo-mesenteric veins, the omphalo-mes teric veins themselves subsequently uniting into a common ven trunk, called the sinus venosus, which is continuous with the pri tive auricle.

This vitelline circulation in the human embryo persists but a sh time. After the fifth or sixth week of fœtal life it becomes obl rated, the yolk then being atrophied, and the placental circulati well developed.

(*b*) The *later*, or *placental circulation*, is developed in the me blastic layer of the allantois, especially in that part which is relation with the decidua serotina. The allantois, when fully veloped, extends to the chorion, over which it spreads, sendi in processes to occupy the villi. These chorionic villi are embed in the decidua of the uterus, and are especially developed at upper part, which is in connection with the decidua serotina maternal placenta.

The primitive aortæ, which were at first two separate tubes, beco united in the dorsal region of the embryo, so that the two ao arches end in a single vessel, which extends to the middle of embryo, and there divides into two branches, each of which gives a vessel called the vitelline or omphalo-mesenteric artery.

From the branches of the aortæ arise two large vessels, wh running along the allantois, spread out over the chorion, be especially directed to the upper part of this membrane; these the umbilical or hypogastric arteries, which carry the blood fr the aortæ to the fœtal placenta.

Veins arise from the terminal networks of these arteries, and co bine to form the two umbilical veins. The umbilical veins tak similar course to the arteries, and convey the blood to the ven trunk formed by the junction of the omphalo-mesenteric veins.

After a time the right umbilical and right omphalo-mesenteric veins disappear, whilst from the trunk formed by the junction of the left umbilical and left omphalo-mesenteric veins, branches are given off to the liver (the *venæ advehentes*), and at a point nearer the heart, vessels are received from the liver (the *venæ revehentes*).

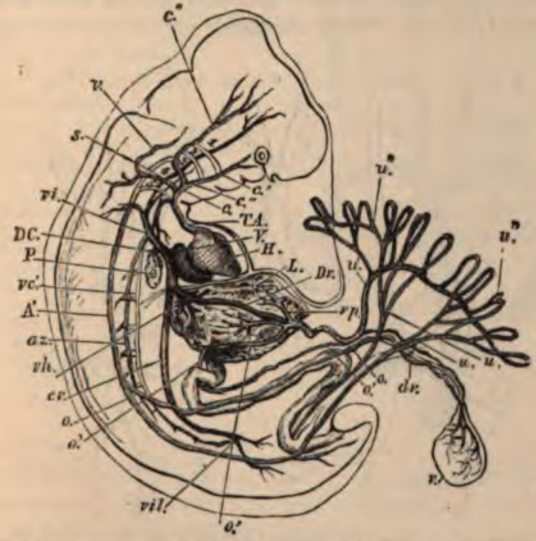


Fig. 267.—Diagram of the vascular system of a human fœtus. (Huxley.)

H. Heart.
T.A. Aortic trunk.
c. Common carotid artery.
c'. External carotid artery.
c''. Internal carotid artery.
s. Subclavian artery.
v. Vertebral artery.
1, 2, 3, 4, 5, Aortic arches.
A'. Dorsal aorta.
1. Omphalo-mesenteric artery.
dv. Vitelline duct.
o'. Omphalo-mesenteric vein.
v'. Umbilical vesicle.
vp. Portal vein.
L. Liver.
uu. Umbilical arteries.
u'' u''. Their endings in the placenta.
u'. Umbilical vein.
Dv. Ductus venosus.
vh. Hepatic vein.
cv. Vena cava inferior.
vil. Iliac veins.
az. Vena azygos.
vc. Posterior cardinal vein.
DC. Duct of Cuvier.
P. Lungs.

To the part of the vessel intervening between the origin of the venæ advehentes and the entrance of the venæ revehentes is given the name of the *ductus venosus.*

Thus it may be seen that in the placental circulation the blood conveyed from the aorta, by the umbilical arteries, to the fœtal placenta, and here it undergoes changes, owing to its close relationship to the maternal blood. From the placenta it is returned by the umbilical vein, which sends a part through the liver and a part direct to the heart. The more minute details of fœtal circulation will be described later on.

The Arterial System.—Around the pharynx are developed five pairs of aortic arches. These commence anteriorly from the two

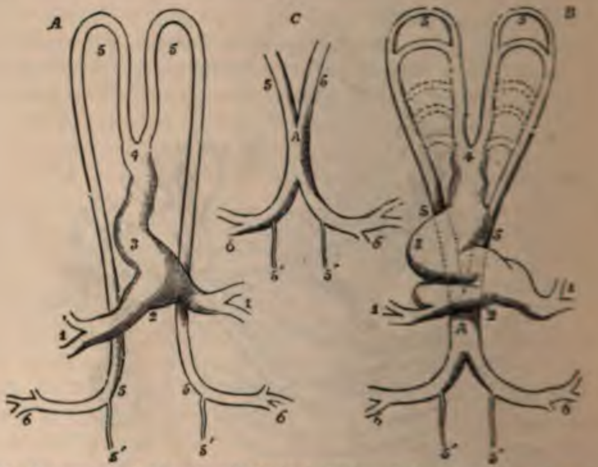


Fig 288.—Diagram of the heart and principal arteries of the chick. (Allen Thomson.)
B. and C. are later than A.

1, 1. Omphalo-mesenteric veins.
2. Auricle.
3. Ventricle.
A. United Aorta.
4. Aortic bulb.
5, 5. Primitive aortæ.
6, 6. Omphalo-mesenteric arteries.

primitive aortæ, and, passing along the side of the pharynx, end in the aortæ as they descend to become united in the dorsal region of the embryo. The points of origin of the arches are termed their anterior roots, and the points of termination their posterior roots.

Though all these arches do not exist at the same time, still, in describing the vessels which arise from them, they may be conveniently considered together.

On the right side the fifth arch disappears completely. On the left side the anterior root and neighbouring part of the fifth arch are transformed into the pulmonary artery; the remaining part of this arch continues as the ductus arteriosus, which connects the pulmonary artery with the permanent aorta.

The fourth left arch, in mammalia, becomes the permanent aorta. At the junction of the fourth and fifth left posterior roots the left subclavian artery is given off. In birds the right fourth arch is transformed into the permanent aorta; and in examining the development of the aortic arch of the chick, it must be borne in mind that it is on the opposite side to that it occupies in man.

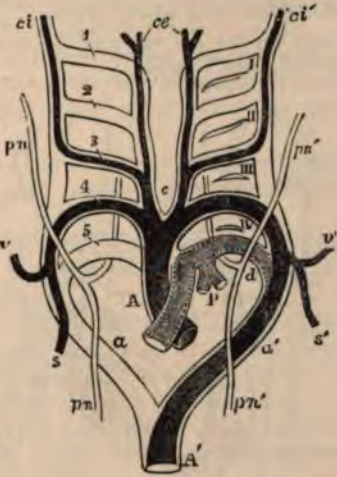


Fig. 289.—Diagram of the aortic arches, the permanent vessels arising from them are shaded darkly. (Allen Thomson after Rathke.)

1, 2, 3, 4, 5, Primitive aortic arches of right side.

I. II. III. IV. Pharyngeal clefts of the left side, showing the relationship of the clefts to the aortic arches.

A. Aorta.
P. Pulmonary artery.
d. Ductus arteriosus.
a' Left aortic root.
a. Right aortic root.
A' descending aorta.
pn. *pn*.' Right and left vagi.
s.*s'*. Right and left subclavian arteries.
v.*v'*. Right and left vertebral arteries.
c. Common carotid arteries.
ce. External carotid.
ci. *ci'*. Right and left internal carotid.

On the right side the anterior root of the fourth arch, and the part of the aortic trunk leading to it, persist as the innominate artery, the fourth arch being represented by the right subclavian artery.

The part of the primitive aortic trunk joining the fourth and third right anterior roots becomes the common carotid artery of the same side, whilst arising from this is the internal carotid, which, taking the position of the third arch, passes to the posterior roots, and occupies the trunk of the primitive aorta from the third to the first arches.

The external carotid, arising from the common carotid at the third anterior root, occupies the position of the vessel joining this root to those of the second and first arch.

On the left side the common carotid and its branches are developed similarly to those on the right, the only difference being that the common carotid arises from the aorta and not from the innominate.

The iliac arteries are developed from the hypogastric. At first they *appear as branches*, but with the growth of the limbs they

become so much larger that after birth they appear to be the m
branches from the point of division of the aorta, the hypogast
arteries now being merely small branches of the iliac vessels.

With the development of the organs and limbs, vessels in conne
tion with those above described arise in the mesoblast. It is, how
ever, beyond the scope of this work to describe in detail the orig
of the lesser vessels.

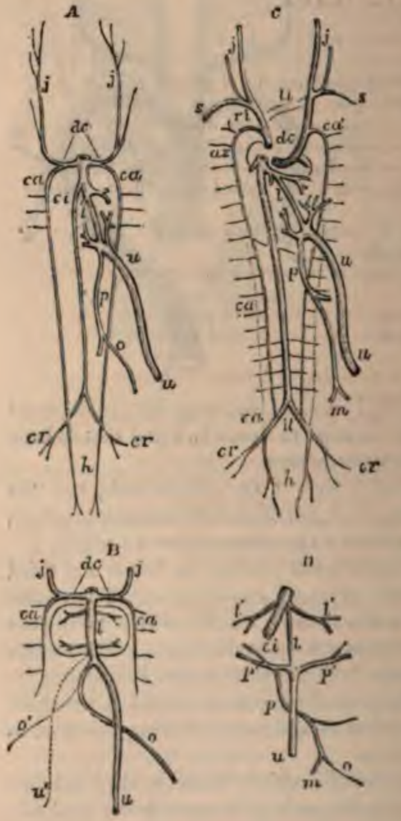


Fig. 290.

A. Plan of principal veins of
foetus of about four we
old.

B. Veins of the liver at an ea
period.

C. Veins after the establish
of the placental circula

D. Veins of the liver at the s
period.

j. Primitive jugular veins.
dc. Ducts of Cuvier.
ca. Cardinal veins.
ci. Inferior vena cava.
l. Ductus venosus.
u. Umbilical vein.
p. Portal vein.
o. Vitelline vein.
cr. External iliac veins.
o'. Right vitelline vein.
u'. Right umbilical vein.
l'. Hepatic veins (venæ r
hentes).
p'p'. Venæ advehentes.
m. Mesenteric veins.
az. Azygos vein.
ca'. Remains of left car
vein.
s. Subclavian vein.
li. Cross branch from left ju
lar which becomes the
brachio-cephalic vein.
ri. Right innominate vein.
s.s. Subclavian veins.
h. Hypogastric veins.
il. Division of inferior vena
into the common
veins.

Venous System.—The blood is returned from the head by
two primitive jugulars, which unite with the cardinal veins conne

the blood from the trunk and lower extremities to form a vessel on each side, called the *duct of Cuvier.*

From the lower extremity of the embryo the inferior vena cava commences by the union of the external iliac veins; this passes up and opens into the venous trunk common to the left vitelline and left umbilical veins.

The left vitelline becomes continuous with the vessels from the common trunk going to the right side of the liver (the right vena advehens), and forms the main trunk of the portal vein (*v.* fig. 290, B. & D.).

At this stage of the formation of the veins there are three trunks opening into the auricle, the right and left ducts of Cuvier and the inferior vena cava.

As development proceeds, the lower parts of the cardinal veins join the external iliac veins, forming the common iliacs, and so return their blood into the inferior vena cava.

The upper parts of the cardinal veins become continuous with the posterior vertebral veins which convey the blood from the parietes of the embryo. Between the latter a communicating branch is established, which helps in the formation of the azygos vein.

The ducts of Cuvier, which at first were placed almost at right angles to the auricle, become more oblique in their direction as the heart descends.

Between the primitive jugular veins a cross branch is developed, which conveys the blood from the left side of the head and upper extremity to the duct of Cuvier of the opposite side.

The left duct of Cuvier, below the communicating branch, atrophies and forms part of the coronary veins of the heart. The connection between this and the vein above the cross branch being, in the adult, represented by a small vein, or a band of fibrous tissue, called the vestigial fold of the pericardium.

The cross branch from the left to the right jugular becomes the left innominate vein. The right duct of Cuvier and the right jugular below the entrance of this cross branch, forms the superior vena cava; whilst the part of the right primitive jugular immediately above the entry of the left innominate vein, forms the right innominate vein.

The posterior vertebral vein of the right side forms the vena azygos major; the corresponding branch of the opposite side, together with the part of the left primitive jugular below the cross branch, forms the left superior intercostal vein and the superior vena *azygos minor.* The lower part of the left posterior vertebral vein,

together with the connecting branch to the right vein, remain
inferior vena azygos minor.

Fœtal Circulation:—The course taken by the blood throu
heart and vessels of the embryo differs essentially from that
persists in adult life.

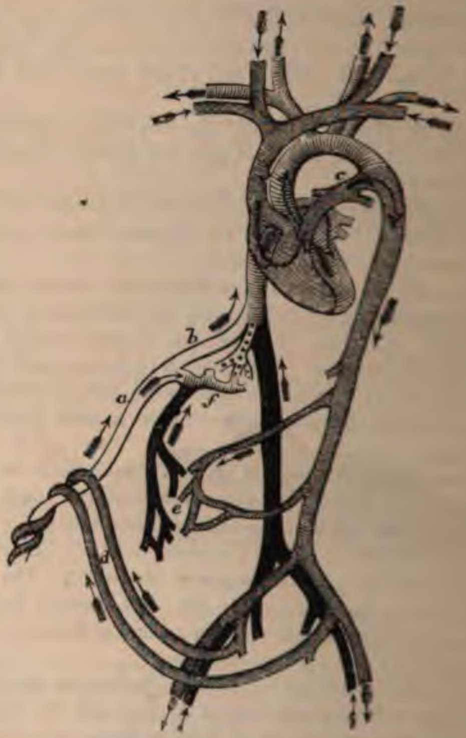


Fig. 291.—Diagram illustrating the circulaton through the heart and the prin
vessels of a fœtus. (Cleland.)

a. umbelical vein.
b. Ductus venosus.
f. Portal vein.
e. Vessels to the viscera.
d. Hypogastric arteries.
c. Ductus arteriosus.

Tracing the blood from the placenta, it passes along the umbi
vein towards the liver, here it may take either of two course
reach the vena cava, one which follows the ductus venosus and av
the liver, the other which passes by the venæ advehentes (portal

to the liver, and proceeds by the venæ revehentes (hepatic veins) to the inferior vena cava, which receives all the blood passing by both of these channels. From this the blood is emptied into the right auricle, and hence is guided by the Eustachian valve through the septum by the patent foramen ovale to the left auricle. From the left auricle it passes to the left ventricle, which contracts and sends the blood into the aortic arch, where it is split up into two streams, one of which passes into the vessels of the head and neck, the other by the descending aorta to the trunk and lower extremities.

The blood from the head and neck is returned to the right auricle by the superior vena cava. The blood from this vein passes through the auricle to the right ventricle, which sends it through the pulmonary artery towards the lungs.

The pulmonary artery, however, in the embryo, has one very large branch, called the ductus arteriosus, which joins the aorta at a point just below the origin of the vessels of the head and neck; hence the main part of the blood passing from the right ventricle reaches the aorta by the ductus arteriosus, and only a very small part goes to the lungs, to be returned from them by the pulmonary veins to the left auricle.

The blood from the ductus arteriosus blends, therefore, with that in the aorta which is passing to the viscera and lower extremities. The main part of this blood travels by two large branches of the aorta (the hypogastric arteries) to the placenta, where it is aerated and purified, &c.

It is evident, then, that as the placenta is the great renovating organ of the blood of the fœtus, that the blood in the umbilical vein is the most arterial in the fœtal circulation. The blood in the ascending vena cava and first part of the aorta is likewise fairly arterial, but the blood in the descending aorta is of a mixed character, as it contains blood which has nourished the head and neck, besides blood which has come from the placenta by the inferior vena cava through the right auricle, foramen ovale, left auricle, and left ventricle.

As the fœtal lungs are not called into play until after birth, but little blood passes to them in the fœtus; this state of things is however completely altered at birth, when the lungs of the child expand, the pulmonary arteries increase in size, and the ductus arteriosus dwindles in a corresponding degree.

The liver, which in the fœtus is of relatively greater size than in the adult, receives much blood coming from the placenta to the heart, and is thought to contribute to it several essential constituents.

The head and brain, which are largely developed in the fœtus, receive well aerated blood; namely, the placental blood which has passed through the liver, and, in the inferior vena cava, is mixed with blood coming from the lower limbs. The rest of the foetus receives blood that is less well aerated, as it is mixed with that which is returned from the head and neck to the right side of the heart, and which is sent through the ductus arteriosus to join the general blood current in the aorta going to the viscera and lower extremities.

DEVELOPMENT OF THE EYE.

The optic vesicles arise from the anterior cerebral vesicle at a very early period, and their cavities are continuous with that of the fore-brain. With the development of the rudimentary cerebral hemispheres the optic vesicles become displaced downwards, and their cavities open into the junction of the cavities of the cerebral hemispheres and that of the thalamencephalon, which becomes the third ventricle. Later, the optic vesicles open directly into the third ventricle, and finally are displaced backwards, and come into connection with the mid-brain.

The optic vesicles are at first hollow prolongations, which consist of an anterior dilated portion, forming the primary optic vesicle, and a posterior tubular portion or stalk joining the vesicle to the fore-brain. This stalk forms the optic nerve.

As each vesicle grows forwards towards the epiblast covering the head of the embryo, the epiblastic cells at the spot overlying the vesicle, become thickened, and an involution of the epiblast takes place towards the optic vesicle, and indents the latter, approximating its anterior to its posterior wall.

By this means the anterior and posterior walls of the primary optic vesicle come into close contact, and the cavity of the vesicle is obliterated. The two layers of the vesicle are now cup-shaped, and receive the name of the secondary optic vesicle or the *optic cup*. This ultimately becomes the retina, and the optic stalk losing its cavity is transformed into the optic nerve.

Meanwhile, the local involution of the epiblast over the optic cup, which is the rudiment of the crystaline lens, becomes gradually separated from the general epiblast giving origin to it, and is finally detached from its point of origin. It now lies as a somewhat spherical body in the cavity of the optic cup within the superficial mesoblast, which has closed over it.

The secondary optic vesicle grows (except at its lower part, just at the junction of the optic stalk), so as to deepen the optic cup.

which contains the rudimentary lens. At the lower part an interval is left, which receives the name of the *choroidal fissure.* Through this gap in the secondary optic vesicle the mesoblast enters and separates the lens from the optic cup, and forms the vitreous humour.

The mesoblast surrounding the optic cup develops two coverings of the eye, an outer fibrous capsule called the sclerotic coat, and a vascular coat, the choroid, which lies in contact with the outer layer of the optic cup.

In front of the lens, beneath the epiblast, the mesoblast forms the corneal tissue proper. The epiblast forms the epithelial or conjunctival covering of the eyeball.

The involution of mesoblast through the choroidal fissure, which forms the vitreous humour, indents the optic stalk, and forms the central artery of the retina. The choroidal fissure is gradually obliterated, and its position may sometimes be marked by a permanent fissure in the iris (*coloboma iridis*).

The rudimentary lens is a spherical body, hollow in the centre, made up of an anterior and posterior wall, each of which is formed of columnar cells. The posterior wall of the lens increases greatly in thickness, and approaching the anterior wall obliterates the original cavity of the lens.

The cells forming this wall become very much elongated, and form long fibre-like columnar cells. The cells of the anterior wall from being a columnar epithelium, are modified to a flattened epithelium, and finally become the layer of epithelium lining the anterior surface of the capsule of the lens. The capsule of the lens has been variously considered as arising from the cells of the lens substance, or as originating from a thin layer of mesoblast, which forms not only the lens capsule, but also the hyaloid membrane, which is continuous with it.

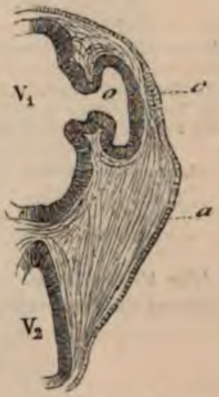


Fig. 292.—Section through the head of a chick at the third day, showing the origin of the lens.

a. Epiblast thickened at *c*, which is the point of origin of the lens.
o. Optic vesicle.
V 1. Anterior cerebral vesicle.
V 2. Posterior cerebral vesicle.

The optic cup gives origin to the retina. The inner or anterior layer of the cup becomes thickened, and from it are differentiated the various layers of the retina, except the layer of pigment cells which lies next to the choroid. The posterior layer develops this layer of pigment cells, which, from their intimate connection to the choroid, were formerly considered as part of that membrane.

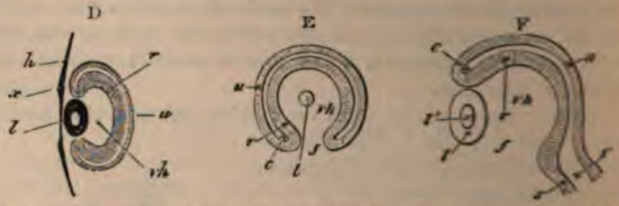


Fig. 293.—Diagrammatic sections of the primitive eye, showing the choroidal fissure. (Foster and Balfour.)

D. Horizontal section.
E. Vertical transverse section just striking the posterior part of the lens.
F. Vertical longitudinal section through the optic stalk, and the fissure through which the mesoblast passes to form the vitreous humour.

h. Superficial epiblast.
x. Point of origin of the lens.
v.h. Vitreous humour.
r. Anterior layer of the optic vesicle.
u. Posterior layer of the optic vesicle.
c. Cavity of the optic vesicle.
f. Choroidal fissure.
s. Optic stalk.
s′. Cavity of the optic stalk.
l. Lens. *l′.* Cavity of the lens.

The thickening of the inner or anterior layer of the optic cup ceases at the ora serrata. The outer layer with its contiguous choroid is thrown into a number of folds—the ciliary processes—and passing in front of the lens, helps to form the iris.

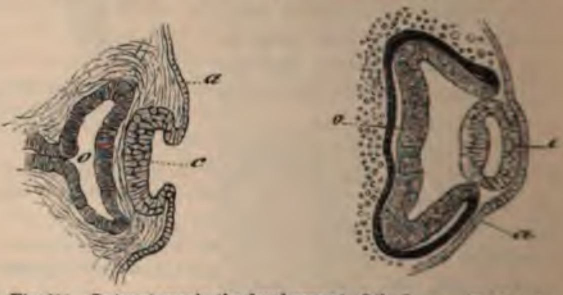


Fig. 294.—Later stages in the development of the lens. (Cadiat.)
a. Epiblast. *c.* Rudimentary lens. *o.* Optic vesicle.

In front of the ora serrata the anterior layer of the cup is no longer differentiated into the special retinal elements, but joins with the posterior to form a layer of columnar cells,—the pars ciliaris retinæ.

In front of this the anterior rim of the optic cup passes forwards and lines the posterior surface of the iris, forming the uvea of that organ, and terminates at the margin of the pupil.

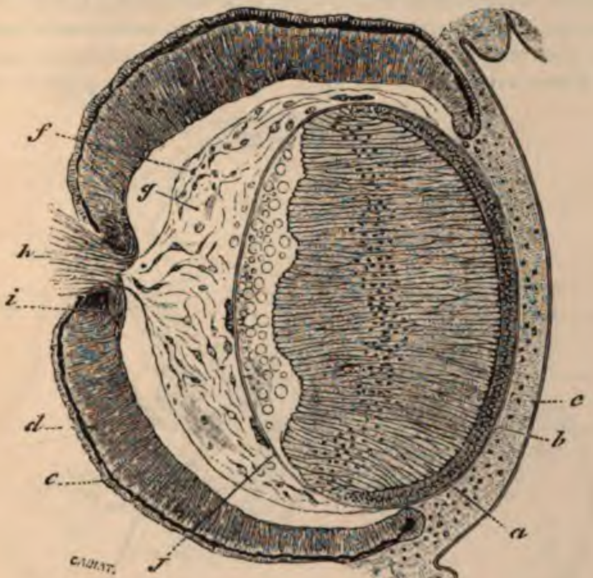


Fig. 295.—A further stage of the development of the lens. (Cadiat.)

a, Elongating epithelial cells forming lens; *b*, Capsule; *c*, Cutaneous tissue becoming conjunctiva; *d*, *e*, Two layers of optic cup forming retina; *f*, Cell of mucous tissue of the vitreous humour; *g*, Intercellular substance; *h*, Developing optic nerve.

The rest of the substance of the iris is developed from the mesoblast, from which also arise the choroid, the cornea and the sclerotic.

The development of the eye may be thus briefly described. An offshoot of nervous matter from the fore-brain, forms the retina and the uvea, and its stalk, or connection with the brain, develops into the optic nerve.

An involution of epiblast which grows into the nervous cup forms the lens, whilst from the adjacent mesoblast the surrounding parts of the eye arise. The vitreous is produced by the mesoblast growing through a fissure in the lower part of the optic cup to fill its cavity.

DEVELOPMENT OF THE EAR.

The ear is developed chiefly from the epiblast, a special and independent involution of which forms both its essential nervous structures, and the general epithelium lining the membranous labyrinth. The mesoblast supplies the surrounding firmer structures, such as the fibrous substance of the inner ear, and the bony parts in which

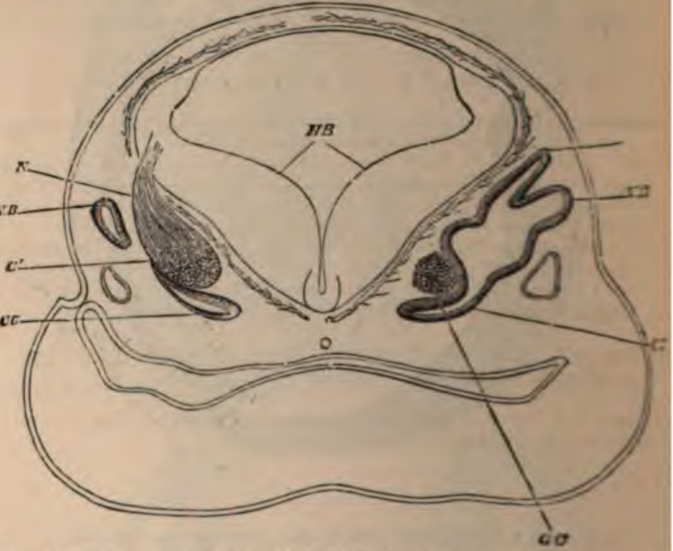


Fig. 296.—Transverse section through the head of a fœtal sheep in the region of t
hind-brain. (Boëttcher.)

H. B. Hind-brain.
CC. Canal of the cochlea.
RC. Recessus vestibuli.
VB. Vertical semicircular canal.
G.C. Auditory ganglion.
G'. Auditory nerve.
X. Connection of auditory nerve to t
hind-brain.

the organ lies. The auditory nerve grows as a bud from the ne
tissue forming the hind-brain, and connects it to the delic
specialised auditory cells.

The process begins by the appearance of a depression of the gene
epiblast covering the head, which soon forms a tubular diverticul
lying in the mesoblast at the side of the hind-brain.

This diverticulum becomes separated from the epiblast by t
obliteration of its outer extremity, which united it to the epibl

epiblast, and is then converted into a cavity and receives the name of the *otic vesicle.* It soon becomes somewhat triangular in shape, the base of the triangle lying upwards.

From the lower angle arises a projection, which is the rudimentary canal of the cochlea. The angle lying next to the neural epiblast similarly gives off a tubular process, which forms the recessus vestibuli.

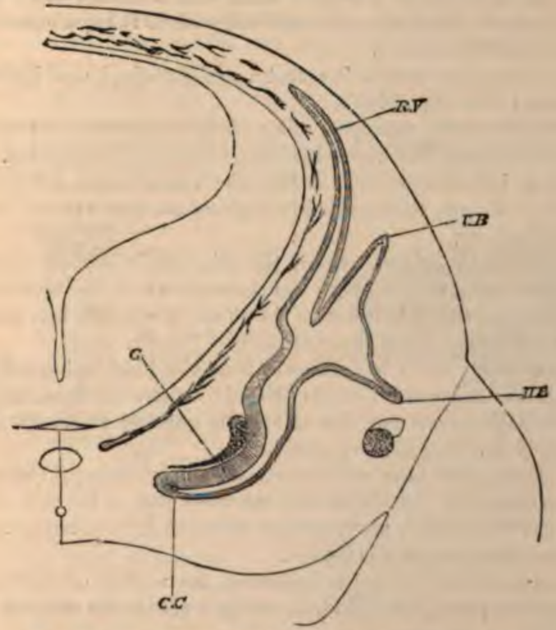


Fig. 297.—Section through the head of a fœtal sheep. (Boëttcher.)

R.V. Recessus vestibuli.
V.B. Vertical Semicircular canal.
H. B. Horizontal semicircular canal.
G. Auditory ganglion.
C.C. Canal of the cochlea.

Elevations in the primitive vesicle indicate the origin of the semicircular canals, which become tubular, opening at their ends into the general cavity of the vesicle. The two superior canals are the first to appear, the horizontal canal rising somewhat later.

The part of the otic vesicle in connection with the canal of the *cochlea becomes* separated from the latter by a narrow constriction which forms the canalis reuniens, the part of the vesicle beyond this developing into the saccule.

The utricle arises from that part of the vesicle which is in connection with the semi-circular canals. It is at first in direct connection with the saccule, but after a time it is only found to communicate by means of a narrow canal with a similar one from the saccule; these two canals are connected with a third, which lies in the aqueductus vestibuli.

The canal of the cochlea is at first a straight tube, but as it develops it becomes coiled upon itself.

The walls of the primitive otic vesicle, formed from the epiblast, become developed into the epithelium lining the internal ear. The mesoblast immediately surrounding the vesicle forms a supporting capsule of fibrous tissue, which completes the membranous parts of the internal ear.

Part of the mesoblast around the otic vesicle becomes liquefied, and gives origin to the canals and spaces in which the membranous labyrinth lies, the neighbouring mesoblast is changed into cartilage which ossifies and forms the bony parts of the ear.

The auditory nerve is developed from the hind-brain, and grows through the mesoblast towards the otic vesicle. It is recognisable from its having some ganglion cells in its growing extremity from a very early period of its development.

The Eustachian tube and the tympanum, or cavity of the middle ear, are formed in connection with the inner part of the first visceral cleft, and the ossicles are developed from the corresponding visceral arch, namely, the *hyo-mandibular*.

The membrana tympani is formed at the surface of the embryo, the adjacent parts grow outwards and give rise to the external auditory meatus.

DEVELOPMENT OF THE SKULL AND FACE.

The bones of the roof of the skull and of the face are chiefly derived from membrane, those of the base of the skull being laid down in cartilage.

At the cephalic extremity of the notochord is a mass of [illegible] mesoblast, called the investing mass, corresponding to that from which the vertebræ are developed.

From this arises two prolongations, which diverge and then unite again, leaving an interval; and the united portion becomes once more divided into two processes, the trabeculæ cranii.

The mesoblast behind the interval receives the name of the [illegible] sphenoid portion; the interval is the rudiment of the sella tunica, which is occupied by the pituitary body. The part of the mesoblast in front of this, is called the spheno-ethmoidal portion.

From the occipito-sphenoidal portion are developed the basi-occipital together with the posterior part of the sphenoid. At the sides of the medulla oblongata processes are sent up, which unite round it and form the foramen magnum. Laterally the mesoblast envelops the auditory vesicles and forms the side portions of the occipital bone.

In the cartilaginous antecedent of the temporal bone there are three centres of ossification—the *epiotic*, which develops the mastoid process; the *proötic*, which is in the region of the superior semicircular canal; and the *opisthotic*, which is at the cochlea.

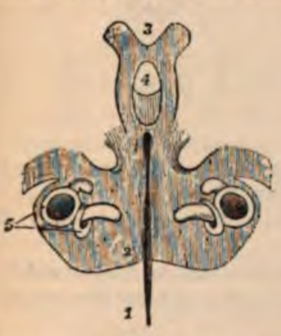


Fig. 298.—Basis cranii of a chick, sixth day. (Huxley.)

3. Trabeculæ.
4. Pituitary space.
1. Notochord.
5. Internal ear.

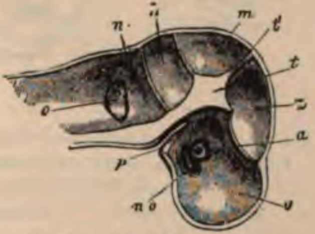


Fig. 299.—Longitudinal section through the head of an embryo of four weeks (Kölliker).

v. Cavity of cerebral hemisphere.
a.no. Optic vesicle.
z. Cavity of third ventricle.
m. Cavity of mid-brain.
h. Cerebellum.
n. Medulla.
o. Auditory depression.
t. Basis cranii.
t'. Tentorium.]
p. Pituitary body.

The spheno-ethmoidal portion develops the anterior part of the sphenoid together with the ethmoid bones and the cartilage of the septum of the nose, the first arising from the back part is developed from membrane. The trabeculæ are carried forwards, and bending down at the nasal depression form the lateral nasal cartilages and the anterior part of the septal cartilage.

The face is developed in connection with ridges known as the *visceral folds* or *arches*, between which are a number of clefts, the *visceral clefts*.

The eyes and the openings of the nose are in the face; whilst the ear arises at the side of the face, in connection with one of the visceral clefts.

The nasal depressions or pits appear in the wall of the head, covering the anterior part of the brain.

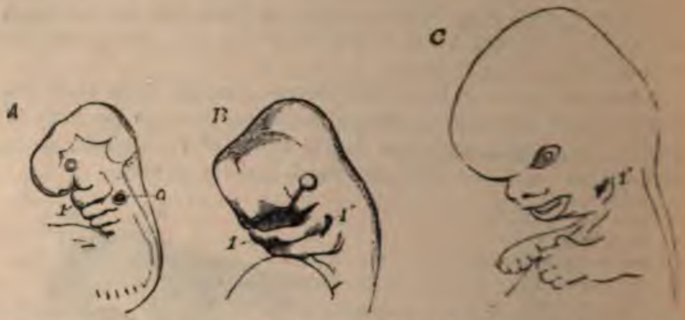


Fig. 300.—Different stages of the development of the head and face of a human embryo.
A. Embryo of four weeks. (Allen Thomson.) B. Embryo of six weeks. (Ecker.)
C. Embryo of nine weeks. (Allen Thomson.)
a. Auditory vesicle. 1. Lower jaw. 1'. First pharyngeal cleft.

Just above the first visceral arch or fold is the depression which ultimately becomes the buccal cavity, and unites with the alimentary tract to form the mouth.

The first fold is called the mandibular; this gives off at either end a process which grows upwards and inwards, forming the rudiment of the superior maxillary bone and side of the face.

Between these is a median process, the fronto-nasal, which gives off, on the inner sides of the nasal grooves, projections which form the inner nasal processes; these unite with the superior maxillary processes to close in the nostril and form the lip.

The outer nasal process is a thickening on the outer side of the nasal depression, which running down towards the superior maxillary process, forms eventually the lachrymal duct.

The mandibular arch forms the lower jaw, and between this and the superior maxillary process the buccal cavity is developed chiefly by the outgrowth of the surrounding tissue; the epiblast lining this becomes thinned away, and the subjacent mesoblast and hypoblast disappear; and thus the buccal cavity is made continuous with that of the alimentary canal.

The cavities of the nasal depressions at first open into the buccal cavity by means of the nasal grooves; after a time, however, processes arise from the superior maxillæ which grow inwards, and finally meet one another in the middle line, forming a broad plate of tissue intervening between the nasal cavity above and the buccal cavity below. The palate when complete in front gradually closes towards the back of the buccal cavity, and here the communication between the nose and the pharynx is left.

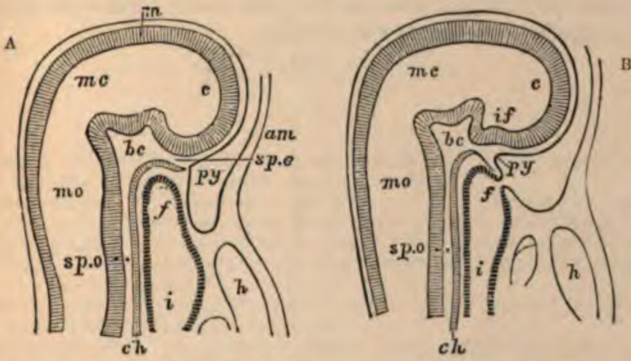


Fig. 301.—Vertical section of the head of an embryo of a rabbit. (Mihalkovics.)

In A. there is no connection between the buccal cavity and the foregut. In B. the connection is established.

m. Epiblast of neural canal.
h. Heart. *c.* Cavity of fore-brain.
mc. Cavity of mid-brain.
mo. Cavity of medulla.
sp.o. Spheno-occipital parts of the basis cranii.
sp.e. Spheno-ethmoidal part of the basis cranii.
bc. Part of basis cranii which receives the pituitary body.
am. Amnion.
py. Part of heart cavity going to form the pituitary body.
i.f. Fore-gut.
ch. Notochord.
if. Infundibulum.

Imperfect development of these parts gives rise to the common congenital deformities, cleft-palate and hare-lip.

The first cleft is the *hyo-mandibular;* it forms the tympano-Eustachian cavity, which becomes separated from the surface by the closure of its outer end by the growth of the membrana tympani, the external auditory meatus and ear being formed by an outgrowth of the tissue surrounding the tympanic membrane.

The mandibular arch contains, close to its connection with the superior maxillary process, a rod of cartilage, called Meckel's cartilage.

This becomes partly converted into the malleus, partly into the internal lateral ligaments of the temporo-maxillary articulation.

The second, or hyoid arch, gives origin to the incus, the stylo-hyoid process and ligament, together with the lesser wings of the hyoid bone.

From the third arch arises the body and greater wings of the hyoid bone together with the thyroid cartilage.

GLOSSARY.

Abscissa. The line forming the basis of measurement of graphic records, along which the time measurement is commonly made.

Accommodation. The focussing of the eye for different distances; it depends upon changes in the lens, which becomes more convex for near objects.

Acinous glands. Secreting organs composed of small saccules filled with glandular epithelium connected with the twigs of a branched duct; like the berries on a bunch of grapes.

Adenoid tissue. The follicular part of lymphatic glands composed of reticular tissue containing the lymph corpuscles.

Adequate stimulus. The particular form of stimulus which excites the nerve-endings of a special sense organ.

Afferent nerves. Nerves bearing impulses to the great nervous centres, from the various parts of the body, so as to give information to the sensorium, or to excite reflex actions.

Agminate glands. A name applied to those lymph follicles that occur in groups in the lower part of the small intestine.

Albumin. A term, derived from the Latin for the white of egg (*albumen*), used in physiology to denote a complex chemical substance which may be obtained from ova, blood-plasma, and many tissues of animals and plants.

Albuminoids. A class of nitrogenous substances allied to the albumins in composition, but differing from them in many important respects.

Allantois. A vascular out-growth from the embryo which in mammals helps to form the placenta, and in birds becomes the respiratory organ of the embryo.

Alveoli. The term used to denote the small cavities found in some parts, such as the air spaces of the lungs.

Amnion. The membranous sac which grows around the embryo and envelops the fœtus while it is being developed *in utero*.

Amœba. A unicellular organism consisting of a nucleated mass of protoplasm.

Amorphous. Without definite or regular form; the opposite of crystalline.

Amylolytic. Relating to the conversion of starch into dextrine and grape sugar.

Amylopsin. A ferment in the pancreatic juice, which converts starch into sugar.

Analgesia. A condition of the nervous centres in which pain cannot be felt, but ordinary tactile and other sensations remain unimpaired.

Analysis. A separation into component parts; the splitting up of a chemical compound into its constituents.

Anastomoses. The direct union of blood-vessels without the intervention of a capillary network.

Anelectrotonus. A peculiar electric condition of a nerve, resulting from the passage of a current through the nerve, but confined to the region where the current enters, *i.e.*, the neighbourhood of the positive pole.

Anode. The positive pole or electrode—*i.e.*, the pole by which the electric current enters a substance.

Apnœa. A state of cessation of the breathing movements from non-excitation of the respiratory nerve centre on account of an unusually arterial state of the blood.

Area opaca. The outer zone of the blastoderm from which the fœtal membranes are developed.

Area pellucida. The central spot of the blastoderm from which the embryo chick is developed.

Arteriole. A small artery; usually applied to those vessels the walls of which are largely composed of muscle tissue.

Arthroses. Movable joints which have a synovial membrane.

Asphyxia. A term meaning, literally, cessation of the pulse, such as occurs from interruption of respiration, now commonly used as synonymous with suffocation.

Assimilation. The chemical combination of new material (nutriment) with living tissues. This forms the most characteristic property of living matter.

Astigmatism. Unevenness of the refracting surfaces of the eye; when engaging the entire cornea, it is called "regular," and affecting a local part, "irregular" astigmatism.

Atoms. The ultimate indivisible particles of matter.

Atrophy. A wasting from insufficient nutrition.

Automatic. Self-moving—*i.e.*, acting without extrinsic aid; a term applied to the independent activity of certain tissues (such as the nerve centres), the exciting energies of which are not readily determined.

Axis cylinder. The essential conducting part of a nerve fibre, which is composed of fine strands of protoplasm.

Bacteria. A class of minute fungi, which occur in all decomposing animal or vegetable substances.

Bilirubin. The red colouring matter of the bile of man and carnivora.

Biliverdin. The greenish colouring matter of the bile of herbivorous animals.

Binocular. Pertaining to vision with two eyes. A combination of the effect of two retinal impressions by means of which the appearances of *distance* and *solidity* are arrived at.

Biology. The science of life.

Blastoderm. The primitive cellular membrane formed by the segmentation of the ovum, in a part of which the embryo is developed.

Blood-pressure. The force exercised by the blood against the walls of the vessels. It is very great in the arteries, and therefore causes a constant stream through the capillaries to the veins.

Canaliculi. Minute channels which connect the small cell spaces or lacunæ of bone with each other, and contain protoplasmic filaments uniting the neighbouring cells.

Carbohydrates. Compounds of carbon, hydrogen, and oxygen, in which the oxygen and hydrogen exist in the proportions requisite to form water.

Cardiograph. An instrument by means of which the heart's impulse is transmitted, through an air tube, from a tambour on the chest wall to another which makes a record on a moving surface by means of a lever.

Catelectrotonus. A peculiar electric state of a nerve in the region where a current passing through it leaves the nerve, *i.e.*, near the negative pole.

Cathode. The negative pole or electrode—*i.e.*, the one by which the electric current leaves a substance through which it is passing.

Centripetal. Afferent.

Centrifugal. Efferent.

Cerebral vesicles. Primitive swellings on the primary neural tube of the early embryo which develop into the brain.

Chemical elements. Substances which cannot be split up into components, and therefore are regarded as simple.

Chlorophyll. The green colouring matter of the cells of plants. It is supposed to be the agent which, under the influence of light, decomposes carbon dioxide and water to form the cellulose and starch of the plant.

Cholesterin. A substance occurring in the bile, white matter of the brain and spinal cord, and in small quantities in many other tissues. Chemically it is a triatomic alcohol.

Chorda dorsalis. The precursor of the vertebral column of the embryo.

Chorion. The outer layer of the membranes of the ovum, part of which becomes vascular, and helps to form the placenta.

Choroid. The vascular coat of the eye-ball.

Chromatic aberration. The alteration of white light into prismatic colours during its passage through an ordinary lens.

Chyle. The fluid absorbed from the small intestines by the lacteals.

Cilia. Minute vibratile processes which occur on the surface cells of the respiratory and many other epithelial membranes.

Circumvallate. Large papillæ situated at the back of the tongue. They are surrounded by a fossa in the walls of which lie taste buds.

Cloaca. The common opening of the genito-urinary organs into the primitive hind gut of the embryo. The cloaca persists in birds.

Colloid. That condition of quasi-dissolved matter in which it will not diffuse through a membrane such as parchment. The opposite of *crystalloid.*

Co-ordination. The adjustment of separate actions for a definite result, as when the nerve-centres cause various distinct muscles to act together and produce complex movements.

Cytod. A term suggested to denote a living protoplasmic unit which has no nucleus.

Decidua reflexa. The outgrowth of the uterine mucous membrane which surrounds the ovum.

Decidua serotina. The part of the modified mucous membrane of the uterus in which the fecundated ovum is lodged.

Decidua vera. The altered mucous membrane of the uterus, which lines that organ during gestation.

Deglutition. The act of swallowing.

Desquamation. The term used to denote the casting off of the outer layer of the skin.

Dialysis. The diffusion of soluble crystalloid substances through membranes such as parchment.

Diastole. The period of relaxation and rest of the heart's muscle.

Dicrotism. The double wave of the arterial pulse. The dicrotic wave is seen on the descending part of the pulse curve.

Dioptric media. Transparent bodies, such as those parts of the eye which so refract the light that images come to a focus on the retina.

Distal. A term used to denote a part relatively far from the centre.

Ductus arteriosus. A short bond of union between the pulmonary artery and the aorta, which in the fœtus carries blood from the right side of the heart into the aorta.

Ductus venosus. A vessel which, in the fœtus, carries blood from the umbilical vein to the vena cava. After birth it becomes a fibrous cord.

Ductus vitello-intestinalis. The union between the yolk sac and the intestine of the embryo.

Dyspnœa. Difficulty of breathing; it is a condition in which inordinate respiratory movements are excited by an unusually venous state of the blood in the respiratory nerve centre.

Ectoderm. The outer layer of simple organisms.

Ectosarc. A term applied to certain unicellular organisms, meaning the outer layer or covering.

Electrodes. The two terminals which are applied to a substance in order to complete the circuit when it is required to pass a current through the substance.

Electrotonus. A peculiar electric state of nerves resulting from the passage of a continuous current through them.

Embryo. The name given to the animal at the earliest period of its development.

Emmetropic. A term applied to the normal eye, in which parallel rays of light are brought to a focus at the retina without accommodation.

Emulsification. The suspension of very fine particles of liquid or solid in a liquid which is not able to dissolve them.

Endoderm. The inner layer of simple organisms.

Endogenous reproduction. The formation of new cells or organisms within the body of the parent individual.

Endolymph. The liquid contained within the membranous labyrinth of the ear.

Endosmosis. The diffusion of a fluid into a vessel through its walls from the exterior.

Endothelium. The single layer of thin cells which lines the serous cavities, the lymphatic and blood-vessels, and all spaces in the connective tissue (mesoblastic lining cells).

Epiblast. The uppermost of the three layers of the blastoderm, from which the epidermis and the nerve-centres are developed.

Epithelium. The non-vascular cellular tissue developed from the epi- and hypoblast of the blastoderm.

Eupnœa. A term used to denote the normal rhythm of respiratory movements in contradistinction from *dyspnœa* and *apnœa*.

Excito-motor. Impulses which, reflexly, call forth motion.

Excito-secretory. Impulses calling forth the activity of gland cells, commonly applied to afferent influences which act reflexly.

Fibrinogen. A form of globulin obtained from serous fluids, which, on being added to a liquid containing serum-globulin, gives rise to the formation of fibrin.

Fibrinoplastin. A term sometimes applied to paraglobulin or serum-globulin.

Filiform. A name given to a certain class of the papillæ of the tongue, the points of which taper off to a thread.

Fœtus. The fully-formed embryo while in the uterus or egg.

Fungiform. A name given to a certain class of papillæ of the tongue, which are shaped like a toadstool.

Galvanometer. An instrument for measuring the direction and strength of electric currents by means of the deflection of a magnetic needle.

Ganglion. A swelling. Chiefly used to denote swellings on nerves which contain nerve corpuscles. Hence any group or mass of nerve cells.

Gastrula. A stage in the development of animals in which they consist of a small sac composed of two layers of cells.

Gemmation. Budding—a process of reproduction in which a bud forms on the parent organism, and finally separates as a distinct being.

Globulin. A form of albumin insoluble in pure water but soluble in weak solutions of common salt.

Glomerulus. A bundle of capillary loops which form part of the Malpighian body of the kidney.

Glycocholic acid. An acid existing in large quantities combined with soda in the bile of herbivorous animals, and in lesser quantities in man.

Glycogen. Animal starch; a substance belonging to the carbohydrates, which is made in the liver. It may be readily converted into grape sugar—from which fact its name is derived.

Gustatory. Pertaining to the sense of taste.

Hæmatin. A dark-red amorphous body containing iron; obtained from the decomposition of the colouring matter of the blood (hæmoglobin).

Hæmin. Hydrochlorate of hæmatin; easily obtained, as small dark crystals, by boiling blood to which some common salt and glacial acetic acid have been added.

Holoblastic. The form of ova the entire yolk of which enters into the process of segmentation.

Homœothermic. Even temperatured—a term applied to those animals that keep up a regular temperature, independent of their surroundings—warm-blooded animals.

Hyaloid. Glass-like; a name given to the delicate membrane enclosing the vitreous humour.

Hydrocarbons. Compounds of carbon and hydrogen. Fats, though containing oxygen in addition, have been considered as hydrocarbons.

Hypermetropic. A term applied to eyes in which the focus of parallel rays of light lies beyond the retina; also called *long sight.*

Hypertrophy. Increased growth from excessive nutrition.

Hypoblast. The undermost of the layers of the blastoderm, from which the pulmonary and alimentary tracts and their glands are formed.

Inhibition. A checking or preventive action exercised by some nervous mechanisms over nerve corpuscles and other active tissues.

Infusoria. A name given to a large class of simple organisms which are found in dirty water.

Irradiation. The phenomenon that bright objects appear larger than they really are. It is due to the extension of the effect of light on the retina to those parts immediately adjacent to where the light rays impinge.

Kymograph. An instrument used for recording graphically the undulations of blood-pressure, measured directly from a blood-vessel by means of a manometer.

Lachrymal. Pertaining to the secretion of tears.

Lacunæ. Small spaces in the substance of bone tissue, occupied during life by the bone-cells. They appear black in sections of dry bone owing to their containing air, which replaces the shrivelled cells.

Latency, or Latent period. The time that elapses between the moment of stimulation and the response given by an active tissue.

Leucin. This is a common product of the decomposition of proteids. It is formed in the later stages of pancreatic digestion.

Leucocytes. A term applied to the white blood-corpuscles and lymph cells.

Lumen. The open space seen on section of a tube, vessel or glandular saccule; the cavity surrounded by the gland-cells, in which the secretion collects.

Lymph. The liquid collected by the absorbent vessels from the tissues; the return flow of the irrigation stream escaping from the blood-vessels to nourish the tissues.

Manometer. An instrument for measuring pressure; made of a U-shaped tube containing liquid, commonly mercury.

Medullary sheath. A soft clear sheath around the axis cylinder of medullated nerves, which, owing to its refracting power, gives them the white appearance.

Menstruation. The monthly change in the mucous membrane of the uterus, which accompanies the discharge of the ovum.

Meroblastic. The form of ova in which the yolk does not undergo complete segmentation, as that of birds.

Mesoblast. The middle of the three layers of the blastoderm from which the connective tissues and vascular apparatus of the embryo are formed.

Metabolism. The intimate chemical changes occurring in the various organs and tissues upon which their nutrition and functions depend.

Metanephros. The hinder portion of the Wolffian duct which develops into the kidney and ureter.

Metazoa. A term used to denote all those animals whose ova undergo division, in contradistinction to Protozoa.

Micrococcus. An extremely minute fungus of a round shape. Micrococci occur in many solutions of decomposing organic matter.

Micturition. The act of voiding urine.

Molecules. The smallest physical particles of matter that can exist in a separate state. They are probably always constituted of two or more atoms.

Morphology. The science which treats of the forms and structure of living beings.

Morula. The stage of development of the ovum after segmentation in which all the young cells are alike, before the blastoderm is formed.

Müllerian duct. An embryonic structure from which are formed the genital passages in the female, viz., Fallopian tube, uterus, and vagina.

Myograph. An instrument for graphically recording muscle contraction.

Myosin. The substance formed by the coagulation of muscle plasma. It is one of the globulins.

Natural nerve currents. The electrical currents passing through an exposed muscle or nerve while in the state of rest.

Neuroglia. The reticular connective tissue which binds together the elements of the nerve-centres.

Non-polarizable electrodes. Specially constructed electric terminals which do not set up secondary currents on application to the moist living tissues.

Notochord. The primitive vertebral axis of the embryo.

Nucleolus. A small spot observable in some nuclei.

Nucleus. A central part of a cell differentiated from the main protoplasm, commonly round, but sometimes elongated as in muscle.

Odontoblasts. Living cells lining the pulp-cavity of the interior of a tooth, and presiding over the growth and nutrition of the dentine.

Olfactory. Pertaining to the special sense of smell.

Omphalo-mesenteric. The vessels connecting the embryonic circulation with the yolk sac, which are early obliterated in the mammalian fœtus.

Ophthalmoscope. An instrument consisting of a small mirror by which the interior of the eye can be illuminated so that the fundus may be viewed.

Optic cup. The involuted optic vesicle which is developed into the retina, &c.

Oxyhæmoglobin. The colouring matter of the red blood-corpuscles.

Paramæcium. A unicellular organism composed of a soft mass of protoplasm enclosed in a firmer case and covered with motile cilia.

Parapeptone. A stage in the formation of peptone produced in gastric digestion.

Pepsin. A ferment existing in the gastric juice which converts proteids into peptones.

Peptone. A form of albumin which is produced during the digestion of proteids ; it is very soluble and diffuses readily through membrane.

Perilymph. The liquid surrounding the membranous labyrinth of the ear.

Peristalsis. The mode of contraction of the muscular walls of certain tubes, as the œsophagus and intestine, the effect of which is to cause a progressive constriction, and so force the contents of the tube onwards.

Phakoscope. An instrument for estimating the changes in the shape of the lens during accommodation by doubling the reflected images with a prism.

Placenta. The intra-uterine organ by means of which the fœtal blood is brought into close relationship to that of the mother, so as to gain nutriment and oxygen and get rid of effete matters.

Plasma. A term meaning anything formed or moulded ; it is applied in physiology to indicate chemically complex kinds of matter which subserve to the formation of the living tissues.

Poikilothermic. Varying in temperature. A term applied to those animals whose temperature varies with that of the surrounding medium—"cold-blooded animals."

Presbyopia. A term denoting the loss of power of accommodation for near vision, which accompanies old age.

Protista. A term used to denote the large group of organisms which remain in the primitive state of a single cell during all their lifetime.

Protococcus. A unicellular vegetable organism, the protoplasm of which contains chlorophyll.

Protoplasm. The substance which gives rise to the primitive vital phenomena, seen in unicellular organisms, and which is the chief agent in executing the functions of all the active tissues.

Protovertebræ. The primitive segments of the mesoblast in the site of the future vertebral column.

Protozoa. The division of the protista which has been assigned to the animal kingdom.

Proximal. A term used to denote a part relatively nearer to the centre.

Pseudopodia. A term applied to the projections thrown out by moving protoplasm, by means of which cells, such as amœbæ, move.

Ptyalin. The ferment of the saliva. In a weak alkaline solution it converts starch into dextrine and sugar.

Reflex action. The activity caused by a ganglion cell reflecting an afferent impulse along an efferent nerve to the neighbourhood of original stimulation.

Refraction. The bending which rays of light undergo when passing obliquely from one medium to another of different density.

Reticulum. A network ; a term applied to the interlacement of fibres, such as is seen in reticulated connective tissue, &c.

Rheoscopic frog. An arrangement by which the change in the electric current of one muscle of a frog is made to act as a stimulus to the nerve of another.

Saponification. The formation of soap; the decomposition of oils or fats by means of alkalis into salts of the fatty acid and glycerine.

Sarcolactic acid. The principal acid in dead muscle. It has a dextro-rotatory power on polarized light, which ordinary lactic acid does not possess.

Sarcolemma. The delicate sheath surrounding the fibres of skeletal muscles.

Sclerotic. The fibrous coat of the eye-ball.

Sensorium. That part of the nerve centres which is supposed to perceive sensory impressions.

Somatopleure. The subdivision of the mesoblast which, with the attached epiblast, forms the body-walls of the embryo.

Specific gravity. The relation of the weight of a given volume of any substance to the weight of an equal volume of distilled water at 4° C.

Spherical aberration. The different degrees of refraction at different parts of a lens giving rise to different focal lengths, and causing an indistinctness of the image.

Sphygmograph. An instrument for obtaining a graphic representation of the pulse-wave by means of a lever applied to the radial artery at the wrist.

Splanchnopleure. The subdivision of the mesoblast which, with the attached hypoblast forms the chief visceral cavities of the embryo.

Sporadic ganglia. Swellings occurring in the course of the peripheral nerves caused by a group of nerve corpuscles.

Steapsin. A ferment existing in the pancreatic juice which causes or aids the saponification of the fats.

Sudoriferous glands. The small tubular glands of the skin which secrete the perspiration.

Summation. The adding together of several single contractions of muscle to form a tetanic contraction; the accumulation of stimuli.

Sutures. Unions formed by the direct apposition of bones without intervening cartilage. They do not permit of motion.

Sympathetic nerve. The ganglionic nervous cord on either side of the vertebral column. It transmits most of the vaso-motor impulses coming from the cerebro-spinal centres.

Symphysis. A form of joint without synovial membrane in which the bones are fixed together by fibro-cartilage.

Synthesis. The artificial building up or construction of a chemical compound from simpler materials. Natural processes are not termed syntheses.

Systole. The period of contraction of the heart's muscle.

Taurocholic acid. An acid existing in combination with soda in the bile of man and of carnivorous animals.

Tetanus. In physiology is used to denote the prolonged contraction of the skeletal muscles which follows rapidly repeated stimulations or nervous impulse.

Thalamencephalon. The part of the anterior cerebral vesicle which is left after the differentiation of the optic lobes and cerebral hemispheres.

Thrombosis. The occlusion of a vessel by a local coagulation of the blood.

Trabeculæ. A term used to denote the supporting bars of tissue that pass through some organs, such as those proceeding from the capsule to the interior of the spleen or lymphatic glands.

Trophic. Relating to nutrition.

Trypsin. A ferment in the pancreatic juice which in alkaline solutions converts proteids into peptones.

Tyrosin. A substance formed together with leucin during pancreatic digestion ; it is also produced by putrefaction of proteids.

Urachus. The bond of union which at an early period connects the urinary bladder with the allantois in the embryo ; it is subsequently obliterated in the fœtus.

Vacuoles. Small cavities such as occur in cells. They are supposed to have important functions in many unicellular organisms.

Vagus. The part of the eighth pair of nerves distributed to the viscera of the thorax and abdomen, it is the great regulating nerve of the vegetative functions.

Vasomotor. The name given to the nervous mechanisms controlling the movements of the muscle-wall of the blood-vessels.

Villus. A hair-like process. A term applied to the small projections characteristic of the small intestine. They contain blood vessels and lacteals, and are important in absorption.

Vitellus. The yolk of the ovum, which in mammals divides completely to form the embryo. In birds only a part divides, and the rest serves to nourish the chick.

Vorticella. Bell animalcule, a bell-shaped unicellular organism with a rudimentary ciliated mouth cavity and rapidly contractile stalk.

Wolffian body. An embryonic structure the forerunner of certain parts of the genito-urinary apparatus.

Zymogen. A peculiar substance existing in the secretion of the pancreas supposed to give rise to the pancreatic ferments.

INDEX.

Abdominal respiration, 268
Abscissa, 383
Absorption, 147
  — methods of, 159
Accelerator nerves of the heart, 225
Accommodation, defects of, 480
  — mechanism of, 478
Acinous glands, 94
Adenoid tissue, 301
Afferent cardiac nerves, 226
  — nerve fibres, 413
Air passages, 263
Air, pressure differences in the, 275
  — volume of, 276
Ampullæ of the semicircular canals, 508
Amylopsin, 126
Albumin, acid, 39
  — alkali, 40
  — coagulated, 40
Albuminates, 39
Albuminoids, 41
Albuminous bodies, 37
Albumins, classification of, 38
  — derived, 39
  — tests for, 38
Alimentary canal, development of, 576
Alimentary tract, 76
Allantoin, 45
Allantois, 555, 559
Alveoli, 275
Amnion, 555
Amœba, 14
  — assimilation of, 59
  — discrimination of, 60
  — movements of, 52, 59
Analgesia, 518
Anastomoses, 227
Anelectrotonus, 423
Animal heat, 353
  — expenditure of, 357
Animal heat, gain of, 357
  — mode of production of, 356
  — nervous control of, 358, 362
  — radiation and conduction of, 358
Animals, food of, 64
Anode, 419
Anus, 90
Anvil bone of ear, incus, 505
Aorta, 207
Aortic arches, 595
Apnœa, 280
Aqueous humour, 469
Area opaca, 553
  — pellucida, 553
Arterial blood, 288
  — pulse, The, 247
  — system in the fœtus, 594
  — tone, 256
Arteries, 228
  — development of the, 595
Arthrosis, 398
Asexual reproduction, 546
Asphyxia, 289, 295, 521
Assimilation, 6
Astigmatism, 482
Atmosphere, composition of the, [illegible], 285
Atoms, 5
Auditory nerve ending, 508
  — nerve, cochlear division of the, 508
Auerbach's plexus, 91
Augmentation of nerve cells, 434
Auricles of the heart, 206
Automatic centres in spinal cord, 515
Automatism, 526
  — of nerve cells, 432
Axis cylinder, 21, 414
  — of spinal cord, 513

Bacteria, 57
— wound infection, 58
Basal ganglia, 538
Basement membrane, 18
Belladonna, action on the eye, 480
Bell animalcule, 61
Bile, 127
— composition of, 133
— ducts, 131
— functions of the, 138
— method of obtaining, 133
— salts, 43
— secretion of, 136
— tests, 135
Bilirubin, 135
Biliverdin, 135
Binocular vision, 498
Blastoderm, 12
— of egg, 551
Blind spot, 489
Blood, amount of, 169
— arterial, 288
— carbon dioxide in the, 194
— change from venous to arterial, 288
— changes in the tissues, 292
— changes in the spleen, 304
— chemical interchanges in respiration, 279
— circulation of the, 204
— circumstances influencing coagulation, 197
— coagulation of, 172, 195
— colouring matter of, 187
— current, velocity of the, 253
— destiny of the red discs, 192
— fibrin of, 172
— fibrin ferment, 175
— fibrin formation, 201
— gases in the, 193, 291
— general characteristics of the, 168
— globin, 192
— hæmatin crystals, 190
— hæmin crystals, 191
— hæmoglobin crystals, 188
— liquor sanguinus, 171
— nitrogen in the, 194
— origin of white corpuscles, 180
— oxygen in the, 194
— plasma, 36, 171
— *plasma, composition of*, 173
— *red corpuscles*, 177
Blood, red corpuscles, development of the, 192
— serum, 173, 176
— spectra of, 189
— tension of gases in the, 292
— Valentine's method, 169
— vascular system, development of, 587
— venous, 288
— Weber's method of estimating amount of, 169
— Welcker's method, 170
— white corpuscles, 178
Blood corpuscles, 171
— corpuscles, action of re-agents on, 183
— corpuscles, method of counting, 185
— corpuscles, size and shape of, 181
Blood-pressure, 234
— changes with respiratory movement, 244
— curve, 242
— measurement of the, 237
— relative height of, 240
— respiratory wave of, 244
— tracing, 257
— variations in the, 241
Blood-vessels, 227
— nervous control of the, 259
— relative capacity of, 231
Bone, 30
Bones of middle ear, 505
Brain, 529, 534
— development of, 573
— effect of stimulation of, 543
— fibres and cells in the, 534
— function of the, 535
— recovery after injury of, 544
— result of removal of parts of, 536, 543
— ventricles of, 529
Breaking shock, 419
Bronchial tubes, 263
Brünner's glands, 141
Buccal cavity, development of the, 609
Butter, 70

Calabar bean, action on the eye, 480
Calamus scriptorius, 279
Camera, 474
Canaliculi, 30
Capillaries, 204, 229
Carbohydrates, 46

Carbonic acid in the atmosphere, 285
 — in expired air, 286
 — gas, 49
Cardiac centre in medulla oblongata, 533
 — nerve centres, 223
Cardiograph, 217
Cartilage, elastic fibro-, 29
 — hyaline, 29
 — ossifying, 31
 — white fibro-, 30
Casein, 40, 314
Catelectrotonus, 423
Cathode, 419
Cell contents, 11
 — modification of original, 13
 — reproduction, 53
 — wall, 8, 10
Cells, 8
 — animal, 9
 — budding of, 54
 — development of, 14
 — differentiated, 13
 — endogenous reproduction of, 54
 — indifferent, 12
 — in spinal cord, automatic action of, 526
 — life history of, 55
 — nerve, 413
 — varieties of, 12
Cellulose, 58
Centrifugal nerves, 413
Centripetal nerves, 413
Cephalic or head fold, 554
Cerebellum, 534
Cerebral functions, localisation of the, 542
 — hemispheres, 534, 541
Cerebrin, 43
Cerebrum, histology of the, 540
Cervix uteri, 563
Chalaza of egg, 551
Changes in pancreatic cells, 123
Cheese, 71
Chemical elements, 5
 — basis of body, 33
 — stimulation of muscle, 375
 — stimulation of nerve, 418
Chloride of sodium, 49
Chlorophyll, 58
Cholesterin, 44, 135
Cholin, 44
Chondrin, 42
Chorda dorsalis, or notochord, 567
Choroid, 466
Chorion, 560
Choroidal fissure, 601
Chromatic aberration, 481
Chyme, 119
Ciliary ganglion, 441
 — muscle, 466
 — processes, 466
Ciliated epithelium of bronchi, 263
Circulation of the blood in the fœtus, 590, 596
Circulation, physical forces of the, 231
Circumvallate papillæ, 94, 460
Cochlea, 507
 — basilar member of, 510
 — development of the, 605
 — nerve endings in the, 508
 — organ of Corti, 510
 — rods of Corti, 510
 — reticulated membrane of, 510
Cold-blooded animals, 353
Colon, 89
Colostrum, 314
Colour perception, 493
Common salt, 49
Complemental air, 277
Complementary colours, 494
Connective tissue corpuscles, 28
Contractile tissues, 23, 25, 365
 — vesicle of paramecium, 61
Convex lenses, 473
Convergence of rays of light, 476
Convulsions, 521
Co-ordination, 536
 — of muscular movements, 520
 — of nerve cells, 431
Cornea, 466
Corpora quadrigemina, 522, 534
 — striata, 538
Corpus callosum, 529
Corpuscles, blood, 171
 — of Hassall, 301
 — Malpighian, 302
 — salivary, 98
Coughing, 283
 — centre, 531
Cranial nerves, 436
Crura cerebri, 537
Crying, 284
Crystalline lens, 469
 — development of the, 470
 — structure of, 471
Curara, 375
Cutaneous desquamation, 319
Cytode, 9

DANIELL's battery, 418
Decidua reflexa, 561
  — serotina, 559
  — vera, 561
Defæcation, mechanism of, 89
Deglutition, 78
  — nervous mechanism of, 83
Depressor nerve, 257
Development, 550
  — of alimentary canal, 576
  — arterial system, 595
  — blood vascular system, 587
  — brain, 573
  — ear, 604
  — eye, 600
  — genito-urinary apparatus, 581
  — heart, 587
  — kidneys, 584
  — liver, 580
  — lungs, 580
  — nose and mouth, 608
  — œsophagus, 580
  — pancreas, 580
  — sexual organs, 585
  — skull and face, 606
  — spinal cord, 571
  — spleen, 580
  — venous system, 596
Dextrose, 46
Diaphragm, 270
Diastole, 213
Diet table, 352
Digestion, mechanism of, 75
Dioptric apparatus, defects of, 481
  — media of eye-ball, 469
Direct vision, 490
Discus proligerus, 549
Drum of the ear, 503
Du Bois Reymond's spring myograph, 382
Ductless glands, 298
Ductus Arteriosus, 206, 594
  — venosus, 593
  — vitello-intestinalis, 559
Dyspnœa, 280

EAR, auditory canal, 503
  — conduction of sound through the, 502
  — *cochlea, 507*
  — *development of the, 604*
Ear, Eustachian tube, 506
  — labyrinth of the, 503, 507
  — nerve endings in the, 508
  — organ of Corti, 510
  — ossicles of, 504
  — semicircular canals, 508
  — tympanum of, 503
  — of birds, 503
  — of fishes, 502
Ectoderm, 15
Ectosarc of paramæcium, 61
Efferent nerve fibres, 413
Effete products, 44
Egg albumin, 38
Egg, development of the, 550
Eggs, 72
Elastin, 42
Electric shock, 418
  — stimulation of muscle, 375
  — stimulation of nerve, 418
Electrodes, non-polarisable, 372
Electrotonus, 422
Embryonic chick, 554
Emmetropic eye, 478
Emulsification, 126
End bulbs (Krause's), 450
Endoderm, 15
Endogenous division of cells, 54
Endolymph of inner ear, 506
Endosarc of paramæcium, 61
Endothelium, 154
Epiblast, 12, 16, 553
Epithelial tissue, 17
Epithelium, ciliated, 19
  — columnar, 19
  — glandular, 19
  — scaly, 19
  — stratified, 18
Equilibration, 536
Eupnœa, 280
Eustachian tube, 506
  — development of the, 606
Excretions, 317
Expiration, 268
  — muscles of, 273
Eye, 465
  — development of the, 600
  — dioptrics of the, 473
  — motor nerve of the, 436
  — range of distinct vision, 478
  — tunics of the, 466
Eye-ball, dioptric media of, 469
Eye-balls, movements of the, 496
  — muscles of the, 497

FACE, development of the, 606
Fallopian tubes, 549
Fats, 47
Fehling's solution, 108
Fever, variations of temperature in, 361
Fibrin, 40, 172
Fibrinogen, 39, 174
Fibrinoplastin, 174
Fibrous tissue, 26
Fick's pendulum myograph, 382
— spring manometer, 243
Filiform papillæ, 94, 460
Fæces, 145
Fœtal circulation, 590, 596
Food, changes in the mouth, 106
— chemical composition of, 66
— inorganic, 66
— organic, 66
— requirements, 65, 346
— special forms of, 67
— suitable proportion for healthy nourishment, 352
— stuffs, ultimate use of, 351
Foramen ovale of fœtal heart, 589
Fovea centralis, 474
Fungiform papillæ, 460

GALL-BLADDER, 137
Galvanometer, 372
Ganglion cells, 21, 429
— in the spinal cord, 513
— heart, 22
— sympathetic, 22
Gastric glands, 111
Gastric juice, action of, 115
— characters of, 112
— method of obtaining, 113
— secretion of, 113
Gastrula, 15
Gelatin, 42, 349
Gemmation, 54
Genito-urinary apparatus, development of, 581
Germ epithelium, 547
Germinal spot, 549
— vesicle, 549
Giddiness, 459
Gills, 262
Glands, agminate, 300
— blood-elaborating, 297
Glands, lachrymal, 309
— mammary, 312
— meibomian, 312
— mucous, 310
— sebaceous, 311
— sudoriferous, 317
Globulin, 39
Glosso-pharyngeal nerve, 442
Glottis, 263, 404
Glycin, 45
Glyco-cholic acid, 43, 134
Glycocoll, 45
Glycogen, 47, 305
— preparation of, 307
Glycogenic function of liver, 305
Gmelin's test for bile, 136
Goblet cells, 20, 156
Graafian follicle, 547
Grape sugar, 46
Gravid uterus, 563
Gustatory nerves, 460

HAMMER bone of ear, malleus, 495
Haversian system, 30
Hearing, 499
Heart, 203
— action of drugs on the, 225
— development of, 587
— innervation of the, 229
— movements of the, 213
— muscle, 209, 367
— muscular fibres of, 208
— rhythm of the, 213
— sounds, 218
— valves of the, 206, 210
— work done by the, 255
Heart beat, cycle of the, 215
Heart's impulse, 217
Heat regulation, 363
Hepatic vein, 129
Hiccough, 284
Hippuric acid, 46
— in urine, 332
Holoblastic ovum, 553
Homœothermic temperature, 353
Hunger and thirst, 458
Hyaloid membrane of eye, 469
Hydrocele fluid, 173
Hydrochloric acid, 49
Hypermetropia, 480
Hypoblast, 12, 16, 553
Hypoglossal nerve, 445

542
ecal valve, 89
505
n, 46
rent gases, 293
ct vision, 491
46
d current, 420
ion coil, Du Bois Reymond's,

rium, 61
tion of nerve cells, 432
tory action, 522
nic bodies, 48
47
ation, 106
tion, 268
forced, 272
tory muscles, 269
llular substance, 11
stal muscles, 271
bular vein, 129
itial absorption, 149
nal absorption, 155
juice, functions of, 143
motion, nervous mechanism of, 91
secretion, 140
secretion, method of obtaining, 142
movements, 87
ne, development of, 578
large, 145
lymph follicles of, 157
putrefactive fermentation in the, 146
structure of small, 140
bular vein, 129
on of the image, 475
tion, 492
rable gases, 293
6, 482

M, 89, 144
397

N, 42, 319
, blood-vessels of, 323
convoluted tubes of, 322
development of the, 584
lomerulus of, 323

Kidney, pyramids of, 323
— structure of the, 321
Kreatin, 45, 337
Kreatinin, 45
— in urine, 332
Kymograph, Ludwig's, 239
— Fick's spring, 243
Kymographic tracing, 257

LABYRINTH of ear, 499, 503, 507
Lachrymal glands, 309
Lacteals, 142, 148, 156
Lactic fermentation, 47
Lactose, 47
Lacunæ, 30
Larynx, 263
— anatomy of, 404
Latent period, 383
Lateral plates of embryo, 568
Laughing, 284
Law of contraction, 427
Lecithin, 43
Lens, crystalline, 469
Leucin, 45, 125
Leucocytes, 178
Levatores costarum, 271
Levers, orders of, 397
Lieberkühn's follicles, 141
Light impressions, 486
Light, stimulation of retina by, 492
Listing's measurements, 476
Liver cells, 130
Liver, development of, 580
— glycogenic function of the, 305
— structure of, 128
Long sight, 480
Lumen of cell, 123
Lungs, 262
Lung sounds, 274, 278
— tissue, 265
Lungs, development of, 580
Lymph and chyle, 163, 297
— corpuscles, 164
— follicles, 157
— movement of the, 165
— spaces in tendon, 149
Lymphatic glands, 151
Lymphatics, 148

MAKING SHOCK, 418
Malassez' apparatus for counting blood corpuscles, 185

Male and female generative elements, origin of, 546
Malleus, 505
Malpighian bodies of spleen, 304
— corpuscles of kidney, 321
Mammary glands, 312
Mastication, 77
Meat, 71
Mechanical stimulation of muscle, 375
— of nerve, 418
Mercurial manometer, 237
Medulla-oblongata as central organ, 530
— as conductor, 528
— decussation of fibres in, 529
— respiratory centre in, 530
— vaso-motor centre in, 531
Medullary canal, 567
— folds, 553, 566
— groove, 553, 567
— sheath, 22, 414
Meibomian glands, 312
Meissner's plexus, 92, 114
Membrane of Reisner, 508
Membranes of the chick, 555
Memory, 542
Menstruation, 561
— and ovulation, 549
Meroblastic ovum, 553
Mesencephalon, the, 535
Mesoblast, 12, 16, 553
Metabolism, 297
Metazoa, 14
Micrococci, 56
Micturition, 340
— nervous mechanism of, 341
Milk, 68
— action of gastric juice on, 118
— composition of, 315
— influence of nervous system on secretion of, 316
— mode of secretion of, 315
Milk sugar, 47, 314
— tests, 70
Mitral valve, 207
Moist chamber, 382
Molecules, 5
Morphology, 1
Morula, 15
— stage of the ovum, 552
Motor nerve roots, 433
Mouth, development of the, 609
Mouth digestion, 94
Movements of the body, 399
Mucin, 41, 310
Mucous glands, 310
— of tongue, 96
— tissue, 26
Müllerian duct, 582
Muscles, antagonistic, 397
— of the eyeball, 496
— of mastication, 78
— origin and insertion of, 396
— synergetic, 397
Muscle, 23
— active state of, 374
— change in form during con
tion, 381
— changes in structure during
traction of, 377
— chemical changes during
traction of, 377
— chemical change in, 369
— chemical composition of, 36
— consistence of, 368
— contraction of, 381
— elasticity of, 369
— electrical changes in, 379
— electric phenomena, 371
— fatigue, 384, 390
— heart, 209
— histology of, 366
— irritability of, 374
— latent period, 383
— maximum contraction, 387
— natural currents in, 371
— negative variation of current,
— non-striated, 23
— passive state of, 368
— plasma, 36, 369
— recording contraction of, 3
— serum, 369
— single contraction, 383
— stimuli, 374
— striated, 23, 366
— summation, 387
— temperature change during
traction, 380
— tetanus, 388
— tone, 390
— unstriated, 395, 366
— variations in the single
tion, 385
— wave of contraction, 386
Muscle plates of embryo, 569
Muscular co-ordination, 520
— stimuli, different forms of,
375
Muscularis mucosæ, 88, 110

Musical notes or tones, 501
Myographs, 382
Myopia, 480
Myosin, 39, 369

NASAL ganglion, 441
Nausea, 458
Negative after image, 491
— variation of muscle current, 379
Nerve, active state of, 417
— ascending and descending currents, 426
— electric properties of, 416
— electric change in, 421
— electrotonus, 422
— force, velocity of, 420
— natural currents in, 417
— optic, 465
— tissue, 20
— roots, 433
— stimulation, negative variation, 421
— stimuli, 418
— terminals, 428
Nerves, afferent, 21, 415
— cranial, 436
— efferent, 21, 415
— excito-motor, 415
— grey, 415
— inhibitory, 415
— intercentral, 415
— mixed, 433
— motor, 415
— reflex, 415
— secretory, 415
— sensory, 415
— special physiology of, 433
— spinal, 433
— vasa-motor, 415
— white, 415
— third pair of, 436
— fourth pair of, 437
— fifth pair of, 439
— sixth pair of, 437
— seventh pair of, 437
— eighth pair of, 442
— ninth pair of, 445
Nerve cells, 21
— functions of, 430
— in retina, 487
— bipolar, 430
— *multipolar, 22, 430*
— *unipolar, 430*
Nerve corpuscles, 413, 428
— endings, 449
— fibres, 21, 413
— chemistry of, 416
— fatigue of, 424
— irritability of, 423
Nerve muscle preparation, 380, 417
Nervous system, 413
— medulla oblongata, 528
— reflex action, 518
— spinal cord, 513
Neurin, 44
Neuroglia, 513
Neuro-muscular cells, 20
Nitrogen, 50
— in expired air, 286
— in the atmosphere, 285
Nose, 463
— development of the, 608
Notochord, 553
Nucleolus, 8
Nucleus, 8, 10
Nutrition, 343
— and food stuffs, 63
— tissue changes, 344

ODONTOBLASTS, 79
Œsophagus, 82
— development of, 580
Olfactory bulb, 463
— mucous membrane, 464
Omphalo-mesenteric vessels, 592
Ophthalmoscope, 485
Optic axis of the eye, 474
— disc, 485
— lobes, 537
— nerve, 488
— nerve, terminals of the, 488
— thalami, 538, 540
— vesicle, 600
Ora serrata, 490
Organ of Corti, 510
Organisms, characters of, 4
— vital characters of, 51
Ossicles of the middle ear, 504
Ossifying cartilage, 31
Osteoblasts, 32
Otic ganglion, 441
— vesicle, 605
Otoliths, 508
Ovary, 548
Ovoid cells, 111
Ovum, 545

Ovum, changes in the, 551
Oxalic acid in urine, 332
Oxygen, 50
  — in expired air, 286
  — in the atmosphere, 285
Oxyhæmoglobin, 37, 289

Paccinian corpuscles, 451
Pain, 457
Pancreas, Development of, 580
  — Structure of, 120
Pancreatic digestion, 124
Pancreatic juice, Composition of, 121
  — Mode of secretion of, 121
Papillæ of tongue, 94, 460
Paraglobulin (fibrinoplastin), 39
Paramæcium, 16, 61
Parapeptone, 116
Parietal cells, 111
Parotid gland, 96
Pavy's solution, 108
Peduncles of cerebrum, 529
Pepsin, 116
Peptic cells, 111
Peptone, 40
  — Conversion of proteid into, 116
  — tests for, 41
Perception, 448
Perilymph of inner ear, 506
Peristaltic contraction of intestine, 85, 92
Perspiration, effect of nervous influence on, 318
  — insensible, 317
  — quantity given off, 318
  — sensible, 318
Pettenkofer's test for bile, 43, 135
Peyer's patch, 158
Phakoscope, 479
Pharynx, muscles of, 80
Placenta, 561, 592
  — functions of the, 564
Plants, food of, 63
Plasmata, 35
Pleura, function of the, 274
Pneumogastric nerves, 281, 443
Pneumothorax, 275
Poikilothermic animals, 353
Poisonous gases, 293
Polarising current, 422
Pons Varolii, 534
Portal blood, 305
  — vein, 128
Portio dura of seventh nerve, 437
  — mollis of seventh nerve, 49
Porus opticus, 488
Positive after image, 491
Potassium chloride, 49
Potatoes, 72
Presbyopia, 480
Primitive groove, 16
  — nerve sheath, 22, 414
  — streak, 566
Products of tissue change, 42
Protamœba, 9
Protagon, 43
Protista, 14
Protococcus, 58
Protoplasm, 4, 10, 35
  — effect of chemical stimulati 53
  — effect of electric stimulation,
  — effect of mechanical irritatio 52
  — effect of temperature on, 52
  — sensitiveness of, 53
  — movements of, 52
Protoplasmic movements, differentia of, 365
Protovertebra, 568
Protozoa, 14
Pseudopodia, 52
Ptyalin, 107
Puerile breathing, 278
Pulmonary capillaries, 288
Pulse, the, 247
  — tracings, 249
  — variations in the, 251
Pupil of eye, 467
Pupil, circumstances affecting the,
  — contraction of, 484
  — dilatation of, 484
Pylorus, 85

Quadratus lumborum, 271

Ranvier's nodes, 21, 414
Receptaculum chyli, 150
Recording apparatus, 238
Recti muscles of the eye, 497
Reflex action, 431
  — experiment on human subj 521
  — experiment on frogs, [illegible]
  — in the spinal cord, [illegible]

Reflex action, theory of, 522
Reflex centres, special, 525
Reflexion, 526
— of nerve cells, 431
Refraction, 473
Refracting media of the eye, 474
Reproduction, 546
Reserve air, 277
Residual air, 277
Respiration, afferent and efferent nerves, 282
— automatic nerve centre, 280
— chemistry of, 285
— differences in male and female, 269, 287
— external, 261
— internal or tissue, 261, 292
— mechanism of, 260
— nervous mechanism of, 278
— of abnormal air, 292
— variations of pressure in, 276
Respirations, rate of, 268
Respiratory centre in medulla oblongata, 530
— gas interchange, 287
— sounds, 278
Restiform bodies, 529
Reticulum, 302
Retina, 469, 477, 485
— stimulation of the, 491
— structure of, 488
Revolving cylinder, 238
Rheoscopic frog, 379
Ribs, 266
Rigor mortis, 393
Ritter's tetanus, 419
Rods and cones, 488
— of Corti, 510
Rotation of the eye-ball, 496

SACCULES of ear, 605
Sacculated glands, 94
Saliva, composition of, 97
Salivary corpuscles, 98
— glands, 95
Salivary secretion, nerve mechanism of, 100
— method of, 99
Saponification, 125
Sarcolactic acid, 378
Sarcous elements, 368
Sarcolemma, 24, 367
Scaleni muscles, 271
Scheiner's experiment, 477
Sclerotic coat of eye, 466
Sebaceous glands, 311
Secretions, 309
Secreting gland cells, changes in, 104
Segmentation in the ovum, 552
Semi-circular canals, 508
— development of the, 605
Semilunar valves, 207
Sensations, general, 457
Sense of touch, 448
Sensorium, 454
Sensory nerve roots, 433
Serratus posticus inferior, 273
Serum albumin, 38
Seventh nerve, 499
Sexual distinction, 584
— organs, development of the, 585
Shivering, 459
Sighing, 284
Sight, long, 480
— short, 480
Skeletal muscles, 396
Skin sensations, 448
Skull and face, development of the, 606
Smell, sense of, 463
Sneezing, 283
— centre, 531
Sobbing, 284
Solar spectrum, 493
Somatopleure, 555
Sound, 499
— amplitude of vibration, 500
— conduction of, 502
— conduction of, through the ear, 505
— conveyance of, in cochlea, 510
— over-tones, 501, 512
— pitch of note, 500
— quality of notes, 501, 512
— rate of, period of vibration, 500
— tone, noise, 511
— tones or musical notes, 501
— transmission of, 501
— transmission of, to the brain, 512
Sounds, classification of, 412
Special reflex centres, micturition, &c., 525
Special senses, 446
— smell, 463
— taste, 460

Special senses, touch, 452
— vision, 465
Spectrum, solar, 493
Speech, 411
Spermatozoa, 546
Sphenopalatine ganglion, 441
Spherical aberration, 481
Sphygmograph, Marey's, 249
Spinal accessory nerve, 442
Spinal cord, 513
— automatic centres in the, 513
— centres presiding over tonic muscular contraction, 526
— co-ordination of movements, 520
— decussation of fibres in the, 517
— development of, 571
— direction of nerve fibres in the, 516
— effect of section of, 517
— ganglion cells in the, 513
— nerve cells in the, 514
— reflex action in the, 518
— sweating centres in the, 526
— vasa-motor centres, 526
— white and grey substance of, 513
Spinal ganglion, 435
Spinal nerves, 433
— anterior and posterior roots of, 516
Spiral lamina of cochlea, 508
Splanchnopleure, 556
Spleen, 301
— changes of blood in, 304
— development of, 580
— functions of the, 303
Splenic pulp, 302
Sputum, 311
Standing, 399
Stapedius muscle of ear, 506
Stapes, 505
Starch, tests for, 108
— into grape sugar, conversion of, 107
Starvation, 344
Stationary air, 277
Steno's duct, 97
Steapsin, 125
Stirrup bone of ear, stapes, 505
Stomach digestion, 110
— epithelium of, 111
— development of, 578
Stomach, structure of, 84
— motion of, 84
— nerve influence on, 85
Striated muscle, 366
Sublingual gland, 96
Submaxillary ganglion, 442
— gland, 96
Sudoriferous glands, 317
Summation, 387, 521
Supra-renal capsule, 299
Suspensory ligament of lens, 469
Sutures, 397
Swallowing, 80
Sweat, chemical composition of, 31
Sweat glands, 317
Sweating centres in spinal cord, 52
Symphysis, 397
Syntonin, 39
Systole, 213

TACTILE nerve endings, 428
Tambour, Marey's, 218
Taste buds, 460
— sense of, 460
Taurin, 45
Tauro-cholic acid, 43, 134
Tegmentum, 538
Temperature, external variations 362
— internal variations of, 361
— maintenance of uniform, 35
— of mammals, 353
— of man, 354
— measurement of, 354
— variations of, 354
Tendon cells, 27
Tensor tympani muscle, 505
Tetanus, 388
Thermic stimulation of muscle, 375
— of nerve, 418
Thermometer, clinical, 354
Thoracic duct, 151
— movements, 267
— respiration, 268
Thorax, 273
— construction of, 263
Thrombosis, 200
Thymus gland, 300
Thyroid body, 299
Tidal air, 277
Tissue changes, 344
Tissues, classification of, 11
— contractile, 363

Titillation, 459
Tone, 511
Tongue, 460
  — papilla of, 94
Tonic contraction, 256
Tooth, crusta petrosa, 77
  — dentine, 77
  — enamel, 77
  — pulp cavity, 77
Torula cerevisia, (yeast plant), 58
Touch corpuscles (Meissner's), 449
  — sense of locality, 452
  — sense of pressure, 454
  — temperature sense, 445
Trabeculæ, 151
  — of spleen, 301
Triangularis sterni, 273
Tricuspid valve, 206
Trigeminus nerve, 439
Trochlear nerve, 437
Trommer's test, 108
Trypsin, 123
Tubuli seminiferi, 547
Tunica adventitia, 227
  — fibrosa, 548
  — granulosa, 549
  — intima, 228
  — media, 227
  — propria, 548
  — vasculosa, 548
Tuning fork, demonstration of vibrations, 500
  — uses of, in measuring time, 382
Tympanic membrane, 503
Tyrosin, 45, 144

Umbilical vessels, 592
Umbilicus, 557
Unicellular organisms, 14
Unstriated muscle, 366, 395
Urachus, 560
Urea, 44, 329
  — source of, 336
  — preparation of, 330
  — volumetric estimation of, 331
Uric acid, 45, 331
Ureters, 339
Urinary calculi, 335
  — excretion, 321
  — secretion, nervous mechanism of, 338
Urine, 325
  — *abnormal constituents of, 334*
Urine, chemical composition of, 329
  — colouring matters of the, 333
  — gases in, 334
  — inorganic salts in, 333
  — passage into bladder, 338
  — specific gravity of, 326
  — secretion of, 326
Uterus, 563
Utricle of ear, 605

Vacuoles, 8
  — of paramæcium, 61
Vagus nerve, 225, 443
  — effect on respiration, 281
  — effect on heart, 224
Valsalva's experiment, 506
Valvulæ conniventes, 140
Vasa-motor centre in medulla oblongata, 531
  — centres in spinal cord, 526
  — nerves, 255
Vascular system, development of, 587
Vas-deferens, development of, 583
Vegetable cells, 8
  — action of light on, 63
Vegetable food, 72
Veins, 230
  — development of the, 593
Velocity of blood current, 252
Venæ advehentes, 593
Vena porta, 305
Venous blood, 288
  — system, development of the, 596
Ventilation, 293
Ventricles of brain, 529
  — of heart, 206
Vesicular breathing, 278
Vestibule of ear, 505
Vertebral plates of embryo, 568
Villi, vessels of, 142
Vision, 465
  — accommodation, 478
  — binocular, 498
  — inversion of image, 475
  — light impressions, 486
  — refraction, 473
Visual perceptions, 495
  — purple, 492
Vital capacity, 277
  — phenomena, 6
  — point (nœud vital), 279
Vitellin, 39

Vomiting, 85
Vorticella, 16, 62
— ciliary motion of, 62
— contractile stalk of, 62

Walking and running, 402
Warm-blooded animals, 353
Water, 48

Yeast plant, 58
Yellow elastic tis
Yellow spot, 486
— structure
Yolk sac, the, 55

Zona pellucida, 5
Zymogen, 124

THE END.

[Catalogue C]

LONDON, *February*, 1884.

J. & A. CHURCHILL'S

MEDICAL CLASS BOOKS.

ANATOMY.

BRAUNE.—An Atlas of Topographical Anatomy, after Plane Sections of Frozen Bodies. By Wilhelm Braune, Professor of Anatomy in the University of Leipzig. Translated by Edward Bellamy, F.R.C.S., and Member of the Board of Examiners; Surgeon to Charing Cross Hospital, and Lecturer on Anatomy in its School. With 34 Photo-lithographic Plates and 46 Woodcuts. Large Imp. 8vo, 40s.

FLOWER.—Diagrams of the Nerves of the Human Body, exhibiting their Origin, Divisions, and Connexions, with their Distribution to the various Regions of the Cutaneous Surface, and to all the Muscles. By William H. Flower, F.R.C.S., F.R.S. Third Edition, containing 6 Plates. Royal 4to, 12s.

GODLEE.—An Atlas of Human Anatomy: illustrating most of the ordinary Dissections and many not usually practised by the Student. By Rickman J. Godlee, M.S., F.R.C.S., Assistant-Surgeon to University College Hospital, and Senior Demonstrator of Anatomy in University College. With 48 Imp. 4to Coloured Plates, containing 112 Figures, and a Volume of Explanatory Text, with many Engravings. 8vo, £4 14s. 6d.

HEATH.—Practical Anatomy: a Manual of Dissections. By Christopher Heath, F.R.C.S., Holme Professor of Clinical Surgery in University College and Surgeon to the Hospital. Fifth Edition. With 24 Coloured Plates and 269 Engravings. Crown 8vo, 15s.

ANATOMY—*continued.*

HOLDEN.—**A Manual of the Dissection of the** Human Body. By Luther Holden, F.R.C.S., Consulting-Surgeon to St. Bartholomew's Hospital. Fifth Edition. By John Langton, F.R.C.S., Surgeon to, and Lecturer on Anatomy at, St. Bartholomew's Hospital. With Engravings. 8vo. [*In preparation.*

By the same Author.

Human Osteology: comprising a Description of the Bones, with Delineations of the Attachments of the Muscles, the General and Microscopical Structure of Bone and its Development. Sixth Edition, revised by the Author and James Shuter, F.R.C.S., late Assistant-Surgeon to St. Bartholomew's Hospital. With 61 Lithographic Plates and 89 Engravings. Royal 8vo, 16s.

ALSO,

Landmarks, Medical and Surgical. Third Edition. 8vo, 3s. 6d.

MORRIS.—**The Anatomy of the Joints of Man.** By Henry Morris, M.A., F.R.C.S., Surgeon to, and Lecturer on Anatomy and Practical Surgery at, the Middlesex Hospital. With 44 Plates (19 Coloured) and Engravings. 8vo, 16s.

The Anatomical Remembrancer; or, Complete Pocket Anatomist. Eighth Edition. 32mo, 3s. 6d.

WAGSTAFFE.—**The Student's Guide to Human** Osteology. By Wm. Warwick Wagstaffe, F.R.C.S., late Assistant-Surgeon to, and Lecturer on Anatomy at, St. Thomas's Hospital. With 23 Plates and 66 Engravings. Fcap. 8vo, 10s. 6d.

WILSON — BUCHANAN — CLARK. — **Wilson's** Anatomist's Vade-Mecum: a System of Human Anatomy. Tenth Edition, by George Buchanan, Professor of Clinical Surgery in the University of Glasgow, and Henry E. Clark, M.R.C.S., Lecturer on Anatomy in the Glasgow Royal Infirmary School of Medicine. With 450 Engravings, including 26 Coloured Plates. Crown 8vo, 18s.

BOTANY.

BENTLEY.—**A Manual of Botany. By Robert** Bentley, F.L.S., M.R.C.S., Professor of Botany in King's College and to the Pharmaceutical Society. With 1185 Engravings. Fourth Edition. Crown 8vo, 15s.

By the same Author.

The Student's Guide to Structural, Morphological, and Physiological Botany. With 680 Engravings. Fcap. 8vo, 7s. 6d.

BENTLEY AND TRIMEN.—**Medicinal Plants:** being descriptions, with original Figures, of the Principal Plants employed in Medicine, and an account of their Properties and Uses. By Robert Bentley, F.L.S., and Henry Trimen, M.B., F.L.S. In 4 Vols., large 8vo, with 306 Coloured Plates, bound in half morocco, gilt edges, £11 11s.

CHEMISTRY.

BERNAYS.—**Notes for Students in Chemistry;** being a Syllabus of Chemistry compiled mainly from the Manuals of Fownes-Watts, Miller, Wurz, and Schorlemmer. By Albert J. Bernays, Ph.D., Professor of Chemistry at St. Thomas's Hospital. Sixth Edition. Fcap. 8vo, 3s. 6d.

By the same Author.

Skeleton Notes on Analytical Chemistry, for Students in Medicine. Fcap. 8vo, 2s. 6d.

BLOXAM.—**Chemistry, Inorganic and Organic;** with Experiments. By Charles L. Bloxam, Professor of Chemistry in King's College. Fifth Edition. With nearly 300 Engravings. 8vo, 16s.

By the same Author.

Laboratory Teaching; or, Progressive Exercises in Practical Chemistry. Fourth Edition. With 83 Engravings. Crown 8vo, 5s. 6d.

CHEMISTRY—*continued.*

BOWMAN AND BLOXAM.—**Practical Chemistry,** including Analysis. By John E. Bowman, formerly Professor of Practical Chemistry in King's College, and Charles L. Bloxam, Professor of Chemistry in King's College. With 98 Engravings. Seventh Edition. Fcap. 8vo, 6s. 6d.

BROWN.—**Practical Chemistry: Analytical** Tables and Exercises for Students. By J. Campbell Brown, D.Sc. Lond., Professor of Chemistry in University College, Liverpool. Second Edition. 8vo, 2s. 6d.

CLOWES.—**Practical Chemistry and Qualitative** Inorganic Analysis. An Elementary Treatise, specially adapted for use in the Laboratories of Schools and Colleges, and by Beginners. By Frank Clowes, D.Sc., Professor of Chemistry in University College, Nottingham. Third Edition. With 47 Engravings. Post 8vo, 7s. 6d.

FOWNES.—**Manual of Chemistry.**—*See WATTS.*

LUFF.—**An Introduction to the Study of Chemistry.** Specially designed for Medical and Pharmaceutical Students. By A. P. Luff, F.I.C., F.C.S., Lecturer on Chemistry in the Central School of Chemistry and Pharmacy. Crown 8vo, 2s. 6d.

TIDY.—**A Handbook of Modern Chemistry,** Inorganic and Organic. By C. Meymott Tidy, M.B., Professor of Chemistry and Medical Jurisprudence at the London Hospital. 8vo, 16s.

VACHER.—**A Primer of Chemistry, including** Analysis. By Arthur Vacher. 18mo, 1s.

VALENTIN.—**Chemical Tables for the Lecture-**room and Laboratory. By William G. Valentin, F.C.S. In Five large Sheets, 5s. 6d.

CHEMISTRY—*continued.*

VALENTIN AND HODGKINSON.—**A Course of Qualitative Chemical Analysis.** By W. G. VALENTIN, F.C.S. Fifth Edition by W. R. HODGKINSON, Ph.D. (Würzburg), Demonstrator of Practical Chemistry in the Science Training Schools. With Engravings. 8vo, 7s. 6d.

WATTS.—**Physical and Inorganic Chemistry.** By HENRY WATTS, B.A., F.R.S. (being Vol. I. of the Thirteenth Edition of Fownes' Manual of Chemistry). With 150 Wood Engravings, and Coloured Plate of Spectra. Crown 8vo, 9s.

By the same Author.

Chemistry of Carbon - Compounds, or Organic Chemistry (being Vol. II. of the Twelfth Edition of Fownes' Manual of Chemistry). With Engravings. Crown 8vo, 10s.

CHILDREN, DISEASES OF.

DAY.—**A Treatise on the Diseases of Children.** For Practitioners and Students. By WILLIAM H. DAY, M.D., Physician to the Samaritan Hospital for Women and Children. Crown 8vo, 12s. 6d.

ELLIS.—**A Practical Manual of the Diseases of Children.** By EDWARD ELLIS, M.D., late Senior Physician to the Victoria Hospital for Sick Children. With a Formulary. Fourth Edition. Crown 8vo, 10s.

SMITH.—**Clinical Studies of Disease in Children.** By EUSTACE SMITH, M.D., F.R.C.P., Physician to H.M. the King of the Belgians, and to the East London Hospital for Children. Second Edition. Post 8vo. [*In preparation.*

By the same Author.

On the Wasting Diseases of Infants and Children. Fourth Edition. Post 8vo, 8s. 6d.

STEINER.—**Compendium of Children's Diseases;** a Handbook for Practitioners and Students. By JOHANN STEINER, M.D. Translated by LAWSON TAIT, F.R.C.S., Surgeon to the Birmingham Hospital for Women, &c. 8vo, 12s. 6d.

DENTISTRY.

SEWILL.—**The Student's Guide to Dental** Anatomy and Surgery. By Henry E. Sewill, M.R.C.S., L.D.S., late Dental Surgeon to the West London Hospital. Second Edition. With 78 Engravings. Fcap. 8vo, 5s. 6d.

STOCKEN.—**Elements of Dental Materia Medica** and Therapeutics, with Pharmacopœia. By James Stocken, L.D.S.R.C.S., late Lecturer on Dental Materia Medica and Therapeutics and Dental Surgeon to the National Dental Hospital, assisted by Thomas Gaddes, L.D.S. Eng. and Edin. Third Edition. Fcap. 8vo, 7s. 6d.

TAFT.—**A Practical Treatise on Operative** Dentistry. By Jonathan Taft, D.D.S., Professor of Operative Surgery in the Ohio College of Dental Surgery. Third Edition. With 134 Engravings. 8vo, 18s.

TOMES (C. S.).—**Manual of Dental Anatomy,** Human and Comparative. By Charles S. Tomes, M.A., F.R.S. Second Edition. With 191 Engravings. Crown 8vo, 12s. 6d.

TOMES (J. and C. S.).—**A Manual of Dental** Surgery. By John Tomes, M.R.C.S., F.R.S., and Charles S. Tomes, M.A., M.R.C.S., F.R.S.; Lecturer on Anatomy and Physiology at the Dental Hospital of London. Third Edition. With many Engravings. Crown 8vo. [*In the press.*

EAR, DISEASES OF.

BURNETT.—**The Ear: its Anatomy, Physiology,** and Diseases. A Practical Treatise for the Use of Medical Students and Practitioners. By Charles H. Burnett, M.D., Aural Surgeon to the Presbyterian Hospital, Philadelphia. With 87 Engravings. 8vo, 18s.

DALBY.—**On Diseases and Injuries of the Ear.** By William B. Dalby, F.R.C.S., Aural Surgeon to, and Lecturer on Aural Surgery at, St. George's Hospital. Second Edition. With Engravings. Fcap. 8vo, 6s. 6d.

EAR, DISEASES OF—*continued.*

JONES.—A Practical Treatise on Aural Surgery. By H. MACNAUGHTON JONES, M.D., Professor of the Queen's University in Ireland, late Surgeon to the Cork Ophthalmic and Aural Hospital. Second Edition. With 63 Engravings. Crown 8vo, 8s. 6d.

By the same Author.

Atlas of the Diseases of the Membrana Tympani. In Coloured Plates, containing 59 Figures. With Explanatory Text. Crown 4to, 21s.

FORENSIC MEDICINE.

OGSTON.—Lectures on Medical Jurisprudence. By FRANCIS OGSTON, M.D., late Professor of Medical Jurisprudence and Medical Logic in the University of Aberdeen. Edited by FRANCIS OGSTON, Jun., M.D., late Lecturer on Practical Toxicology in the University of Aberdeen. With 12 Plates. 8vo, 18s.

TAYLOR.—The Principles and Practice of Medical Jurisprudence. By ALFRED S. TAYLOR, M.D., F.R.S. Third Edition, revised by THOMAS STEVENSON, M.D., F.R.C.P., Lecturer on Chemistry and Medical Jurisprudence at Guy's Hospital; Examiner in Chemistry at the Royal College of Physicians; Official Analyst to the Home Office. With 188 Engravings. 2 Vols. 8vo, 31s. 6d.

By the same Author.

A Manual of Medical Jurisprudence. Tenth Edition. With 55 Engravings. Crown 8vo, 14s.

ALSO,

On Poisons, in relation to Medical Jurisprudence and Medicine. Third Edition. With 104 Engravings. Crown 8vo, 16s.

TIDY AND WOODMAN.—A Handy-Book of Forensic Medicine and Toxicology. By C. MEYMOTT TIDY, M.B.; and W. BATHURST WOODMAN, M.D., F.R.C.P. With 8 Lithographic Plates and 116 Wood Engravings. 8vo, 31s. 6d.

HYGIENE.

PARKES.—A Manual of Practical Hygiene. By Edmund A. Parkes, M.D., F.R.S. Sixth Edition by F. De Chaumont, M.D., F.R.S., Professor of Military Hygiene in the Army Medical School. With 9 Plates and 103 Engravings. 8vo, 18s.

WILSON.—A Handbook of Hygiene and Sanitary Science. By George Wilson, M.A., M.D., F.R.S.E., Medical Officer of Health for Mid Warwickshire. Fifth Edition. With Engravings. Crown 8vo, 10s 6d.

MATERIA MEDICA AND THERAPEUTICS.

BINZ AND SPARKS.—The Elements of Therapeutics: a Clinical Guide to the Action of Medicines. By C. Binz, M.D., Professor of Pharmacology in the University of Bonn. Translated and Edited with Additions, in conformity with the British and American Pharmacopœias, by Edward I. Sparks, M.A., M.B., F.R.C.P. Lond. Crown 8vo, 8s. 6d.

OWEN.—A Manual of Materia Medica; incorporating the Author's "Tables of Materia Medica." By Isambard Owen, M.D., Lecturer on Materia Medica and Therapeutics to St. George's Hospital. Crown 8vo, 6s.

ROYLE AND HARLEY.—A Manual of Materia Medica and Therapeutics. By J. Forbes Royle, M.D., F.R.S., and John Harley, M.D., F.R.C.P., Physician to, and Joint Lecturer on Clinical Medicine at, St. Thomas's Hospital. Sixth Edition. With 139 Engravings. Crown 8vo, 15s.

THOROWGOOD.—The Student's Guide to Materia Medica and Therapeutics. By John C. Thorowgood, M.D., F.R.C.P., Lecturer on Materia Medica at the Middlesex Hospital. Second Edition. With Engravings. Fcap. 8vo, 7s.

WARING.—A Manual of Practical Therapeutics. By Edward J. Waring, C.I.E., M.D., F.R.C.P. Third Edition. Fcap. 8vo, 12s. 6d.

MEDICINE.

BARCLAY.—**A Manual of Medical Diagnosis.** By A. Whyte Barclay, M.D., F.R.C.P., late Physician to, and Lecturer on Medicine at, St. George's Hospital. Third Edition. Fcap. 8vo, 10s. 6d.

CHARTERIS.—**The Student's Guide to the** Practice of Medicine. By Matthew Charteris, M.D., Professor of Materia Medica, University of Glasgow; Physician to the Royal Infirmary. With Engravings on Copper and Wood. Third Edition. Fcap. 8vo, 7s.

FENWICK.—**The Student's Guide to Medical** Diagnosis. By Samuel Fenwick, M.D., F.R.C.P., Physician to the London Hospital. Fifth Edition. With 111 Engravings. Fcap. 8vo, 7s.

By the same Author.

The Student's Outlines of Medical Treatment. Second Edition. Fcap. 8vo, 7s.

FLINT.—**Clinical Medicine: a Systematic Treatise** on the Diagnosis and Treatment of Disease. By Austin Flint, M.D., Professor of the Principles and Practice of Medicine, &c., in Bellevue Hospital Medical College. 8vo, 20s.

HALL.—**Synopsis of the Diseases of the Larynx,** Lungs, and Heart: comprising Dr. Edwards' Tables on the Examination of the Chest. With Alterations and Additions. By F. De Havilland Hall, M.D., F.R.C.P., Assistant-Physician to the Westminster Hospital. Royal 8vo, 2s. 6d.

SANSOM.—**Manual of the Physical Diagnosis** of Diseases of the Heart, including the use of the Sphygmograph and Cardiograph. By A. E. Sansom, M.D., F.R.C.P., Assistant-Physician to the London Hospital. Third Edition. With 47 Woodcuts. Fcap. 8vo, 7s. 6d.

WARNER.—**Student's Guide to Medical Case-**Taking. By Francis Warner, M.D., F.R.C.P., Assistant-Physician to the London Hospital. Fcap. 8vo, 5s.

WEST.—**How to Examine the Chest: being a** Practical Guide for the Use of Students. By Samuel West, M.D., M.R.C.P., Physician to the City of London Hospital for Diseases of the Chest, &c. With 42 Engravings. Fcap. 8vo, 5s.

MEDICINE—*continued.*

WHITTAKER.—**Students' Primer on the Urine.** By J. Travis Whittaker, M.D., Clinical Demonstrator at the Royal Infirmary, Glasgow. With Illustrations, and 16 Plates etched on Copper. Post 8vo, 4s. 6d.

MIDWIFERY.

BARNES.—**Lectures on Obstetric Operations,** including the Treatment of Hæmorrhage, and forming a Guide to the Management of Difficult Labour. By Robert Barnes, M.D., F.R.C.P., Obstetric Physician to, and Lecturer on Diseases of Women, &c., at, St. George's Hospital. Third Edition. With 124 Engravings. 8vo, 18s.

CLAY.—**The Complete Handbook of Obstetric** Surgery; or, Short Rules of Practice in every Emergency, from the Simplest to the most formidable Operations connected with the Science of Obstetricy. By Charles Clay, M.D., late Senior Surgeon to, and Lecturer on Midwifery at, St. Mary's Hospital, Manchester. Third Edition. With 91 Engravings. Fcap. 8vo, 6s. 6d.

RAMSBOTHAM.—**The Principles and Practice** of Obstetric Medicine and Surgery. By Francis H. Ramsbotham, M.D., formerly Obstetric Physician to the London Hospital. Fifth Edition. With 120 Plates, forming one thick handsome volume. 8vo, 22s.

REYNOLDS.—**Notes on Midwifery: specially** designed to assist the Student in preparing for Examination. By J. J. Reynolds, L.R.C.P., M.R.C.S. Fcap. 8vo, 4s.

ROBERTS.—**The Student's Guide to the Practice** of Midwifery. By D. Lloyd Roberts, M.D., F.R.C.P., Physician to St. Mary's Hospital, Manchester. Third Edition. With Engravings. Fcap. 8vo. [*In the Press.*

SCHROEDER.—**A Manual of Midwifery; including** the Pathology of Pregnancy and the Puerperal State. By Karl Schroeder, M.D., Professor of Midwifery in the University of Erlangen. Translated by Charles H. Carter, M.D. With Engravings. 8vo, 12s. 6d.

MIDWIFERY—*continued.*

SWAYNE.—**Obstetric Aphorisms for the Use of** Students commencing Midwifery Practice. By Joseph G. Swayne, M.D., Lecturer on Midwifery at the Bristol School of Medicine. Seventh Edition. With Engravings. Fcap. 8vo, 3s. 6d.

MICROSCOPY.

CARPENTER.—**The Microscope and its Revelations.** By William B. Carpenter, C.B., M.D., F.R.S. Sixth Edition. With 26 Plates, a Coloured Frontispiece, and more than 500 Engravings. Crown 8vo, 16s.

MARSH.—**Microscopical Section-Cutting: a** Practical Guide to the Preparation and Mounting of Sections for the Microscope, special prominence being given to the subject of Animal Sections. By Dr. Sylvester Marsh. Second Edition. With 17 Engravings. Fcap. 8vo, 3s. 6d.

MARTIN.—**A Manual of Microscopic Mounting.** By John H. Martin, Member of the Society of Public Analysts, &c. Second Edition. With several Plates and 144 Engravings. 8vo, 7s. 6d.

OPHTHALMOLOGY.

HIGGENS.—**Hints on Ophthalmic Out-Patient** Practice. By Charles Higgens, F.R.C.S., Ophthalmic Surgeon to, and Lecturer on Ophthalmology at, Guy's Hospital. Second Edition. Fcap. 8vo, 3s.

JONES.—**A Manual of the Principles and** Practice of Ophthalmic Medicine and Surgery. By T. Wharton Jones, F.R.C.S., F.R.S., late Ophthalmic Surgeon and Professor of Ophthalmology to University College Hospital. Third Edition. With 9 Coloured Plates and 173 Engravings. Fcap. 8vo, 12s. 6d.

MACNAMARA.—**A Manual of the Diseases of** the Eye. By Charles Macnamara, F.R.C.S., Surgeon to, and Lecturer on Surgery at, Westminster Hospital. Fourth Edition. With 4 Coloured Plates and 66 Engravings. Fcap. 8vo, 10s. 6d.

OPHTHALMOLOGY—*continued.*

NETTLESHIP.—**The Student's Guide to Diseases** of the Eye. By EDWARD NETTLESHIP, F.R.C.S., Ophthalmic Surgeon to, and Lecturer on Ophthalmic Surgery at, St. Thomas's Hospital. Third Edition. With many Engravings, and a Set of Coloured Papers illustrating Colour-blindness. Fcap. 8vo. [*In the press.*

WOLFE.—**On Diseases and Injuries of the Eye:** a Course of Systematic and Clinical Lectures to Students and Medical Practitioners. By J. R. WOLFE, M.D., F.R.C.S.E., Senior Surgeon to the Glasgow Ophthalmic Institution, Lecturer on Ophthalmic Medicine and Surgery in Anderson's College. With 10 Coloured Plates, and 120 Wood Engravings, 8vo.

PATHOLOGY.

JONES AND SIEVEKING.—**A Manual of Pathological Anatomy.** By C. HANDFIELD JONES, M.B., F.R.S., and EDWARD H. SIEVEKING, M.D., F.R.C.P. Second Edition. Edited, with considerable enlargement, by J. F. PAYNE, M.B., Assistant-Physician and Lecturer on General Pathology at St. Thomas's Hospital. With 195 Engravings. Crown 8vo, 16s.

LANCEREAUX.—**Atlas of Pathological Anatomy.** By Dr. LANCEREAUX. Translated by W. S. GREENFIELD, M.D., Professor of Pathology in the University of Edinburgh. With 70 Coloured Plates. Imperial 8vo, £5 5s.

VIRCHOW. — **Post-Mortem Examinations:** a Description and Explanation of the Method of Performing them, with especial reference to Medico-Legal Practice. By Professor RUDOLPH VIRCHOW, Berlin Charité Hospital. Translated by Dr. T. B. SMITH. Second Edition, with 4 Plates. Fcap. 8vo, 3s. 6d.

WILKS AND MOXON.—**Lectures on Pathological Anatomy.** By SAMUEL WILKS, M.D., F.R.S., Physician to, and late Lecturer on Medicine at, Guy's Hospital; and WALTER MOXON, M.D., F.R.C.P., Physician to, and Lecturer on the Practice of Medicine at, Guy's Hospital. Second Edition. With 7 Steel Plates. 8vo, 18s.

PSYCHOLOGY.

MANN.—**A Manual of Psychological Medicine** and Allied Nervous Disorders. By EDWARD C. MANN, M.D., Member of the New York Medico-Legal Society. With Plates. 8vo, 24s.

PSYCHOLOGY—*continued.*

BUCKNILL AND TUKE.—**A Manual of Psychological Medicine**: containing the Lunacy Laws, Nosology, Ætiology, Statistics, Description, Diagnosis, Pathology, and Treatment of Insanity, with an Appendix of Cases. By John C. Bucknill, M.D., F.R.S., and D. Hack Tuke, M.D., F.R.C.P. Fourth Edition, with 12 Plates (30 Figures). 8vo, 25s.

CLOUSTON. — **Clinical Lectures on Mental Diseases.** By Thomas S. Clouston, M.D. and F.R.C.P. Edin., Lecturer on Mental Diseases in the University of Edinburgh. With 8 Plates (6 coloured). Crown 8vo, 12s. 6d.

PHYSIOLOGY.

CARPENTER.—**Principles of Human Physiology.** By William B. Carpenter, C.B., M.D., F.R.S. Ninth Edition. Edited by Henry Power, M.B., F.R.C.S. With 3 Steel Plates and 377 Wood Engravings. 8vo, 31s. 6d.

DALTON.—**A Treatise on Human Physiology**: designed for the use of Students and Practitioners of Medicine. By John C. Dalton, M.D., Professor of Physiology and Hygiene in the College of Physicians and Surgeons, New York. Seventh Edition. With 252 Engravings. Royal 8vo, 20s.

FREY.—**The Histology and Histo-Chemistry of Man.** A Treatise on the Elements of Composition and Structure of the Human Body. By Heinrich Frey, Professor of Medicine in Zurich. Translated by Arthur E. Barker, Assistant-Surgeon to the University College Hospital. With 608 Engavings. 8vo, 21s.

SANDERSON.—**Handbook for the Physiological Laboratory**: containing an Exposition of the fundamental facts of the Science, with explicit Directions for their demonstration. By J. Burdon Sanderson, M.D., F.R.S.; E. Klein, M.D., F.R.S.; Michael Foster, M.D., F.R.S.; and T. Lauder Brunton, M.D., F.R.S. 2 Vols., with 123 Plates. 8vo, 24s.

SURGERY.

BRYANT. — **A Manual for the Practice of Surgery.** By Thomas Bryant, F.R.C.S., Surgeon to, and Lecturer on Surgery at, Guy's Hospital. Fourth Edition. With nearly 700 Engravings (nearly all original, many being coloured). 2 vols. Crown 8vo. [*In the press.*

SURGERY—*continued.*

BELLAMY.—The Student's Guide to Surgical Anatomy; a Description of the more important Surgical Regions of the Human Body, and an Introduction to Operative Surgery. By EDWARD BELLAMY, F.R.C.S., and Member of the Board of Examiners; Surgeon to, and Lecturer on Anatomy at, Charing Cross Hospital. Second Edition. With 76 Engravings. Fcap. 8vo, 7s.

CLARK AND WAGSTAFFE. — Outlines of Surgery and Surgical Pathology. By F. LE GROS CLARK, F.R.C.S., F.R.S., Consulting Surgeon to St. Thomas's Hospital. Second Edition. Revised and expanded by the Author, assisted by W. W. WAGSTAFFE, F.R.C.S., Assistant-Surgeon to St. Thomas's Hospital. 8vo, 10s. 6d.

DRUITT. — The Surgeon's Vade-Mecum; a Manual of Modern Surgery. By ROBERT DRUITT, F.R.C.S. Eleventh Edition. With 369 Engravings. Fcap. 8vo, 14s.

FERGUSSON.—A System of Practical Surgery. By Sir WILLIAM FERGUSSON, Bart., F.R.C.S., F.R.S., late Surgeon and Professor of Clinical Surgery to King's College Hospital. With 463 Engravings. Fifth Edition. 8vo, 21s.

HEATH.—A Manual of Minor Surgery and Bandaging, for the use of House-Surgeons, Dressers, and Junior Practitioners. By CHRISTOPHER HEATH, F.R.C.S., Holme Professor of Clinical Surgery in University College and Surgeon to the Hospital. Seventh Edition. With 129 Engravings. Fcap. 8vo, 6s.

By the same Author.

A Course of Operative Surgery: with Twenty Plates drawn from Nature by M. LÉVEILLÉ, and Coloured. Large 8vo, 40s.

ALSO,

The Student's Guide to Surgical Diagnosis. Second Edition. Fcap. 8vo, 6s. 6d.

MAUNDER.—Operative Surgery. By Charles F. MAUNDER, F.R.C.S., late Surgeon to, and Lecturer on Surgery at, the London Hospital. Second Edition. With 164 Engravings. Post 8vo, 6s.

SURGERY—*continued.*

PIRRIE.—The Principles and Practice of Surgery. By William Pirrie, F.R.S.E., late Professor of Surgery in the University of Aberdeen. Third Edition. With 490 Engravings. 8vo, 28s.

SOUTHAM.—Regional Surgery: including Surgical Diagnosis. A Manual for the use of Students. Part I., the Head and Neck. By Frederick A. Southam, M.A., M.B. Oxon, F.R.C.S., Assistant-Surgeon to the Royal Infirmary, and Assistant-Lecturer on Surgery in the Owen's College School of Medicine, Manchester. Crown 8vo, 6s. 6d.

TERMINOLOGY.

DUNGLISON.—Medical Lexicon: a Dictionary of Medical Science, containing a concise Explanation of its various Subjects and Terms, with Accentuation, Etymology, Synonymes, &c. By Robley Dunglison, M.D. New Edition, thoroughly revised by Richard J. Dunglison, M.D. Royal 8vo, 28s.

MAYNE.—A Medical Vocabulary: being an Explanation of all Terms and Phrases used in the various Departments of Medical Science and Practice, giving their Derivation, Meaning, Application, and Pronunciation. By Robert G. Mayne, M.D., LL.D., and John Mayne, M.D., L.R.C.S.E. Fifth Edition. Fcap. 8vo, 10s. 6d.

WOMEN, DISEASES OF.

BARNES.—A Clinical History of the Medical and Surgical Diseases of Women. By Robert Barnes, M.D., F.R.C.P., Obstetric Physician to, and Lecturer on Diseases of Women, &c., at, St. George's Hospital. Second Edition. With 181 Engravings. 8vo, 28s.

COURTY.—Practical Treatise on Diseases of the Uterus, Ovaries, and Fallopian Tubes. By Professor Courty, Montpellier. Translated from the Third Edition by his Pupil, Agnes M'Laren, M.D., M.K.Q.C.P. With Preface by Dr. Matthews Duncan. With 424 Engravings. 8vo, 24s.

DUNCAN.—Clinical Lectures on the Diseases of Women. By J. Matthews Duncan, M.D., F.R.C.P., F.R.S.E., Obstetric Physician to St. Bartholomew's Hospital. Second Edition, with Appendices. 8vo, 14s.

WOMEN, DISEASES OF—*continued.*

EMMET. — The Principles and Practice of Gynæcology. By Thomas Addis Emmet, M.D., Surgeon to the Woman's Hospital of the State of New York. With 130 Engravings. Royal 8vo, 24s.

GALABIN.—The Student's Guide to the Diseases of Women. By Alfred L. Galabin, M.D., F.R.C.P., Obstetric Physician and Lecturer on Obstetric Medicine at Guy's Hospital. Third Edition. With 78 Engravings. Fcap. 8vo, 7s. 6d.

REYNOLDS.—Notes on Diseases of Women. Specially designed to assist the Student in preparing for Examination. By J. J. Reynolds, L.R.C.P., M.R.C.S. Second Edition. Fcap. 8vo, 2s. 6d.

SMITH.—Practical Gynæcology: a Handbook of the Diseases of Women. By Heywood Smith, M.D., Physician to the Hospital for Women and to the British Lying-in Hospital. With Engravings. Second Edition. Crown 8vo. [*In preparation.*

WEST AND DUNCAN.—Lectures on the Diseases of Women. By Charles West, M.D., F.R.C.P. Fourth Edition. Revised and in part re-written by the Author, with numerous additions, by J. Matthews Duncan, M.D., F.R.C.P., F.R.S.E., Obstetric Physician to St. Bartholomew's Hospital. 8vo, 16s.

ZOOLOGY.

CHAUVEAU AND FLEMING.—The Comparative Anatomy of the Domesticated Animals. By A. Chauveau, Professor at the Lyons Veterinary School; and George Fleming, Veterinary Surgeon, Royal Engineers. With 450 Engravings. 8vo, 31s. 6d.

HUXLEY.—Manual of the Anatomy of Invertebrated Animals. By Thomas H. Huxley, LL.D., F.R.S. With 158 Engravings. Post 8vo, 16s.

By the same Author.

Manual of the Anatomy of Vertebrated Animals. With 110 Engravings. Post 8vo, 12s.

WILSON.—The Student's Guide to Zoology: a Manual of the Principles of Zoological Science. By Andrew Wilson, Lecturer on Natural History, Edinburgh. With Engravings. Fcap. 8vo, 6s. 6d.